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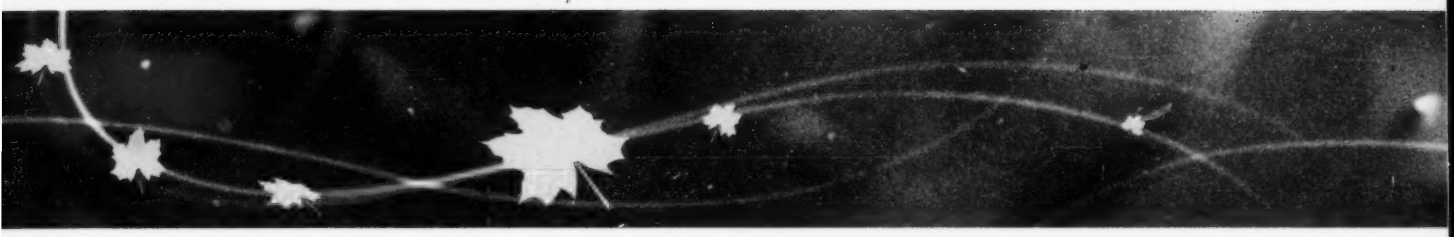
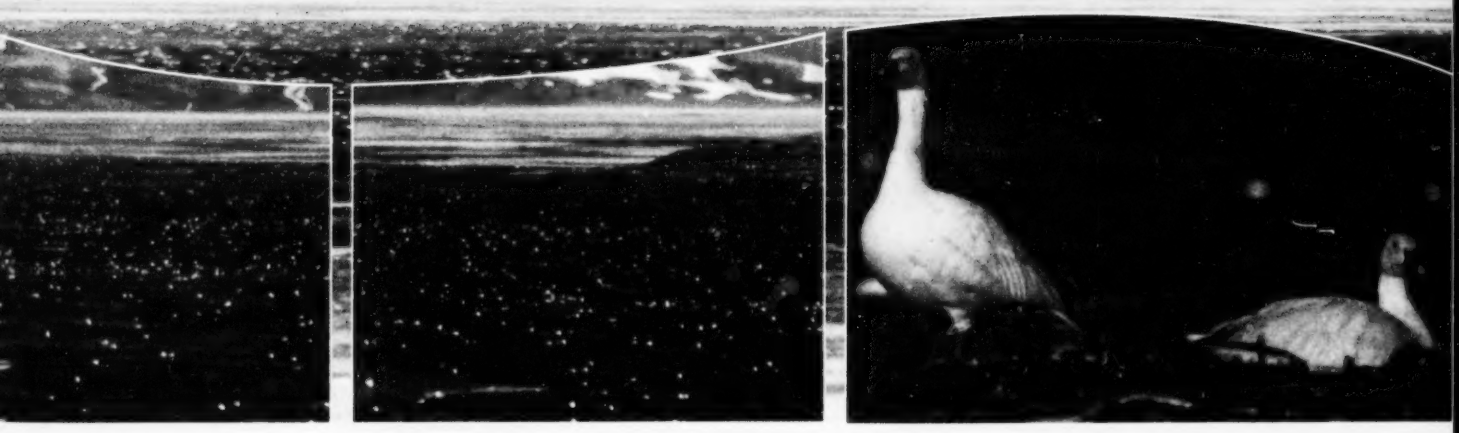


Productivity of Lesser Snow Geese on Banks Island, Northwest Territories, Canada, in 1995–1998

Gustaf Samelius
Ray T. Alisauskas
James E. Hines

Occasional Paper
Number 115
Canadian Wildlife Service



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Productivity of Lesser Snow Geese on Banks Island, Northwest Territories, Canada, in 1995–1998

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Abstract

We estimated that 264 000–452 000 Lesser Snow Geese *Chen caerulescens caerulescens* nested at Egg River on Banks Island, Northwest Territories, in 1995–1998. This was about twice as many geese as was reported nesting there in the 1980s, and we estimated that the nesting population grew by 4.2% per year from 1953 to 1998. The number of nesting geese varied considerably among years and was lower in years when nesting was delayed by late snowmelt (called late years hereafter). Late years were also characterized by large numbers of nonbreeding geese in the brood-rearing areas, suggesting that timing of snowmelt had a greater effect on the proportion of geese attempting to breed at Egg River each year than it had on the number of geese arriving at Banks Island.

Clutch size and nesting success at Egg River ranged between 3.5 and 3.8 eggs and between 45% and 86%, respectively, in 1995–1998. Both clutch size and nesting success were lower in years when nesting was delayed by late snowmelt, which suggests that depletion of body reserves while waiting for snow to melt was a key factor affecting breeding performance at Egg River. Clutch size and nesting success at Egg River were comparable to those of Lesser Snow Geese at other colonies of similar latitude. Lesser Snow Geese at Egg River laid more eggs outside of nest bowls in late years.

We estimated that about 1–4% of the nesting population died at Egg River from 1996 to 1998 (goose mortality was not monitored accurately in 1995). There appeared to be more geese dying in late years, which suggests that deaths were related to the nutritional status of geese. There were likely several causes of death, but avian cholera was confirmed in about half of the dead geese examined in all years. Avian cholera was, thus, an important factor affecting Lesser Snow Geese nesting on Banks Island in all years.

We estimated that 441 000–644 000 adult Lesser Snow Geese were dispersed throughout Banks Island Migratory Bird Sanctuary No. 1 during the brood-rearing season in 1996–1998 (the area was not completely surveyed in 1995, so we were unable to estimate the total number of geese in that year). The highest densities of brood-rearing geese were found in the river valleys closest to Egg River, whereas failed and nonbreeding geese moved farther and were found in the highest density in the delta of Bernard River about 125 km north of Egg River. Even though densities were generally lower on the uplands between river valleys, the vast area of the uplands (80% of the study area) meant that most geese were associated with ponds, lakes, creeks, and small rivers on the uplands.

Gosling survival ranged between 27% and 44% during the first 2–3 weeks after hatch in 1996–1998 and was similar to, or perhaps somewhat lower than, gosling survival of Lesser Snow Geese at other colonies. Goose use had a strong negative impact on the availability of graminoid plants (i.e., grasses and sedges) in the brood-rearing areas of Banks Island Migratory Bird Sanctuary No. 1. However, we did not observe any evidence of permanent destruction of habitats, even though there were indications that areas with high use by geese were heavily grazed, particularly in the colony itself.

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1. Introduction

Lesser Snow Geese *Chen caerulescens caerulescens* of the Pacific Flyway breed at large colonies on Banks Island, Anderson River, and Kendall Island in the Northwest Territories, Howe Island in Alaska, and Wrangel Island in Russia (Kerbes 1986; Johnson 1996; Kerbes et al. 1999). The most recent population estimates for these colonies are 480 000, 3000, 3000, 1000, and 40 000 nesting geese, respectively (Johnson 1996; Kerbes et al. 1999). Geese from these colonies share common wintering grounds in California, in Mexico, in New Mexico, and on the Fraser River in British Columbia and the Skagit River in Washington (Dzubin 1979; Kerbes et al. 1999), where there is interchange of birds from different colonies (Syroechkovsky et al. 1994).

Lesser Snow Geese nesting on Banks Island are of great importance to the Inuvialuit; geese make up an important part of local diets and are harvested by five of six communities in the Inuvialuit Settlement Region (Bromley 1996). Additionally, this population also forms the bulk of geese harvested in the Pacific Flyway (see Kerbes et al. 1999). Survival of Lesser Snow Geese nesting on Banks Island is known from banding studies (e.g., Kerbes et al. 1999), whereas productivity of these birds is poorly documented (but see McEwen 1958).

This study was initiated to provide information on the productivity of Lesser Snow Geese from Banks Island. Our objectives were to:

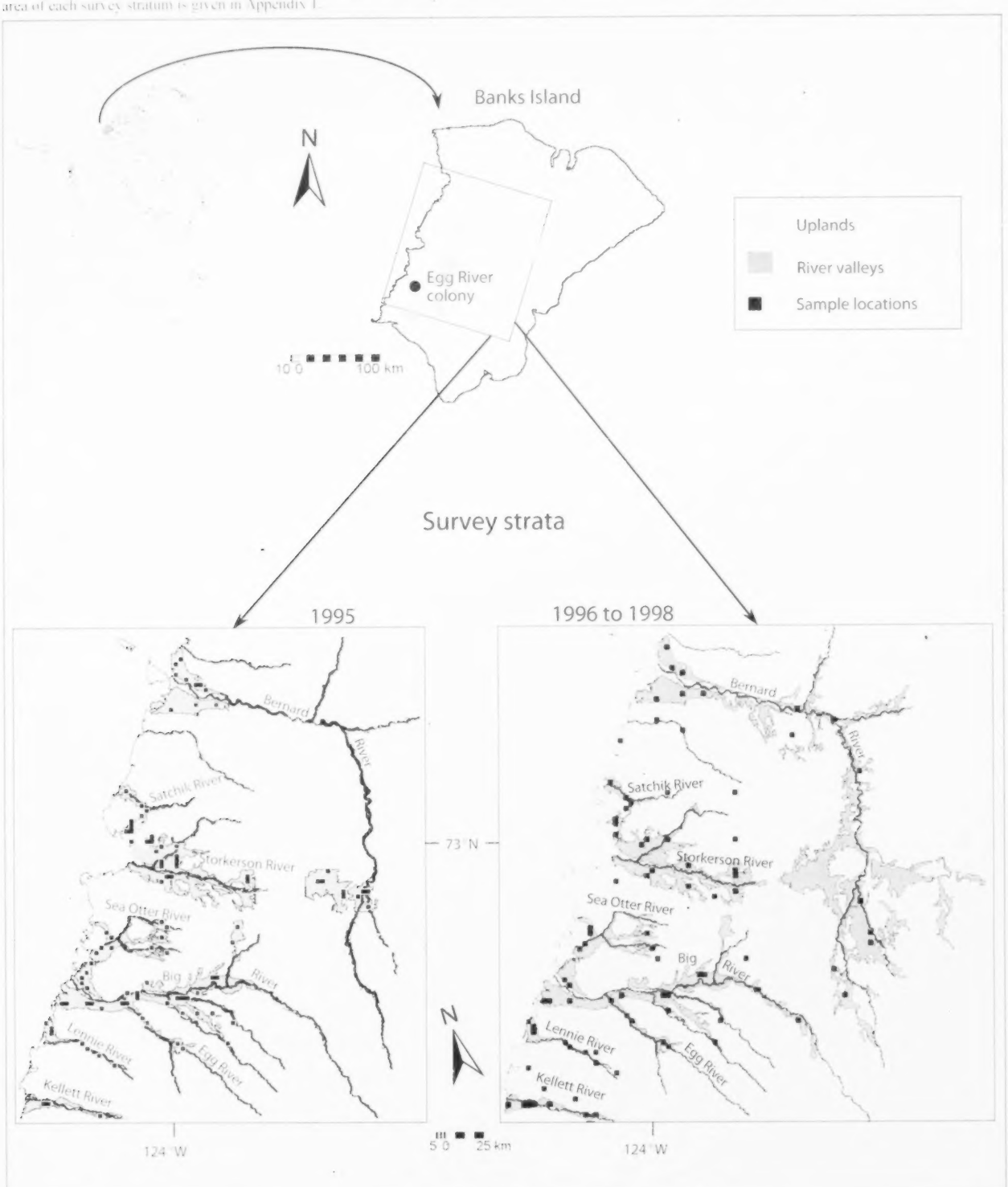
- gather information on the number of nesting geese, nesting success, and gosling survival;
- evaluate the impact of weather and predation on the productivity of geese; and
- determine the impact of grazing by geese on plant communities.

2. Study area

This study was done at the Egg River colony (72°25′N, 124°32′W) and the brood-rearing areas of Banks Island Migratory Bird Sanctuary No. 1 during the summers of 1995–1998 (Fig. 1). Egg River contains over 90% of the Lesser Snow Geese nesting on Banks Island (Kerbes et al. 1999). At Egg River, geese nest in the large valleys of the Egg and Big rivers, with average nesting densities of 29–43 nests/ha in 1995–1998 (see section 4.1.1 below). The nesting grounds are characterized by gravel hills and polygon areas in the southern part of the colony and wet areas with shallow lakes and ponds in the northern part of the colony (see McEwen 1958). After hatch, geese disperse throughout the southwest part of Banks Island (McEwen 1958). This area is composed of gently rolling uplands that are separated by large river valleys, which, in turn, contain numerous lakes and ponds (Cotter and Hines 2001).

In addition to Lesser Snow Geese, other birds observed nesting in the Egg River area during this study included Brant *Branta bernicla*, King Eiders *Somateria spectabilis*, Pacific Loons *Gavia pacifica*, Tundra Swans *Cygnus columbianus*, Sandhill Cranes *Grus canadensis*, Glaucous Gulls *Larus hyperboreus*, Long-tailed Jaegers *Stercorarius longicaudus*, Rough-legged Hawks *Buteo lagopus*, Willow Ptarmigans *Lagopus lagopus*, and Lapland Longspurs *Calcarius lapponicus*. In addition to nesting birds, we also saw Sabine's Gulls *Xema sabini*, Pomarine Jaegers *Stercorarius pomarinus*, Parasitic Jaegers *Stercorarius parasiticus*, Snowy Owls *Bubo scandiacus*, American Golden-Plovers *Pluvialis dominica*, unidentified shorebirds (Charadriiformes spp.), occasional Common Ravens *Corvus corax*, and one Cackling Goose *Branta hutchinsii* in or near the colony. Mammals common in the colony were arctic foxes *Alopex lagopus*, collared lemmings *Dicrostonyx torquatus*, and muskoxen *Ovibus moschatus*. Wolves *Canis lupus*, caribou *Rangifer tarandus*, and arctic hares *Lepus arcticus* were seen occasionally in or near the colony.

Figure 1
Location of Egg River and extent of aerial surveys on Banks Island Migratory Bird Sanctuary No. 1 in 1995–1998. We surveyed all major river valleys of the sanctuary every year and the uplands in between river valleys in 1996–1998. Aerial surveys in 1996–1998 covered the whole sanctuary except for a narrow strip south of Kellett River. Uplands are marked in light grey on the map for the 1996–1998 survey strata. Sample locations are marked with black squares. The area of each survey stratum is given in Appendix 1.



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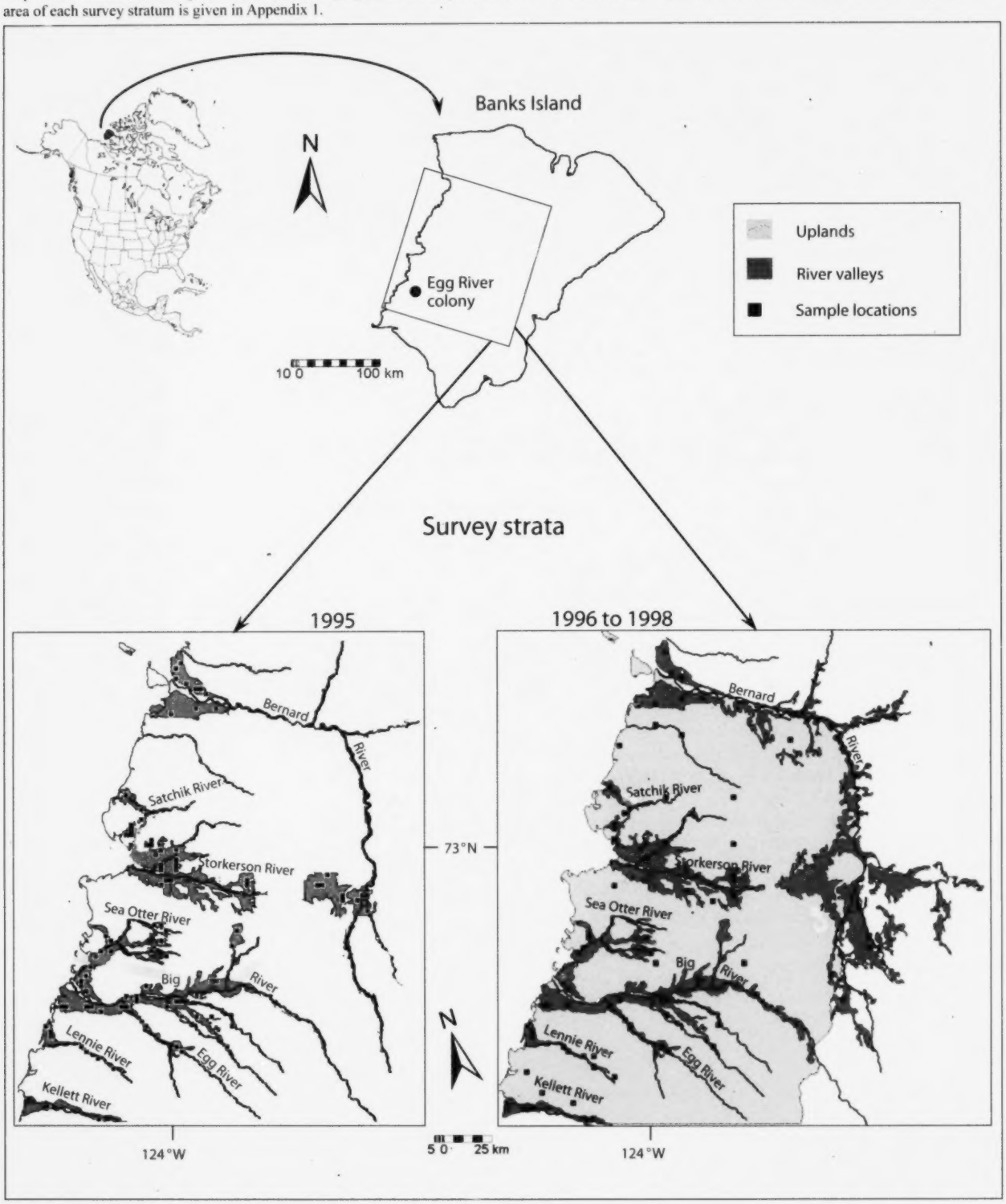


3. Methods

3.1 Nesting ecology

3.1.1 Nest sample plots

We monitored the nesting performance of geese at sample plots distributed systematically throughout the colony in a 1-km grid (the colony varied considerably in size among years, with n = 75, 87, 33, and 72 plots/year in 1995–1998, respectively). The location of sample plots was selected from the Universal Transverse Mercator (UTM) grid system on 1:50 000-scale maps. Sample plots were circular, with a radius of 25 m in 1995 and 30 m in 1996–1998. We started to use sample plots with a 30-m radius in 1995; however, as the number of nests was high (up to 43 nests/plot), we decreased the radius to 25 m to avoid keeping birds away from their nests for too long. In 1996–1998, when less information was recorded at each nest plot (i.e., we did not measure length and width of eggs), we reverted to sample plots with a 30-m radius.

On each sample plot, we recorded the number of nests, the number of eggs per nest, and the number of dead geese (nests were marked uniquely with 13-cm wooden markers). We monitored the presence of nests within 200 m of sample plots if there were no nests on the plot (see definition of the colony in section 3.1.2 below). Nesting mortality was not monitored accurately in 1995, as we did not realize how quickly dead geese were scavenged by predators. However, after 1995, we assumed that goose carcasses that looked fresh or still had some fresh flesh were from geese that died in that year. Otherwise, if carcasses looked weathered or consisted of only bones with few feathers, we assumed that geese had died in a previous year. Dead geese were removed from nest plots to avoid double-counting at later visits. We determined the fate of nests after hatch, with successful nests defined as nests in which one or more goslings hatched. Successful hatching of goslings was determined by the presence of egg membranes or egg caps in the nest bowl or immediately beside the nest bowl (see Ely and Raveling 1984).

We monitored snow cover, nest initiation, clutch size, nesting success, and chronology of adult nesting mortality on a subset of nest plots (called initiation plots hereafter) every 2–5 days throughout the nesting season (n = 22 initiation plots in 1995 and 19 initiation plots in 1996–1998). Initiation plots were located in one section of the colony rather than randomly distributed throughout the colony due to the logistics of travelling (travel on foot was very slow during snowmelt). However, we suggest that these plots accurately represented the whole colony because they covered a continuous section of 22–58% of the colony in each year and included both peripheral and central parts of the colony. Initiation plots were visited every 2–4 days during egg laying and every 4–5 days after egg laying was completed (variation in frequency of visits resulted from us not visiting plots when it rained or snowed). Nest initiation dates were calculated by subtracting 1.4 days from the date of detection for every egg present in a nest when first detected, and incubation was defined to start with the last egg laid (Cooke et al. 1995). Nests were considered active if new eggs had been laid since our last visit or if eggs were warm from incubation. If no new eggs were laid or if eggs were cold, we classed nests as failed. Following Mayfield (1975), we assumed that nesting failure occurred halfway between visits.

3.1.2 Estimate of number of nesting geese

We estimated the number of nesting geese (defined as the number of geese entering incubation) by using Program Distance (Thomas et al. 2002). This program estimates detection probability as a function of search area (the search area of sample plots increased exponentially as the radius of sample plots increased) and the number of nesting geese as the product of nesting density and the area used by nesting geese. We defined nesting geese as those that entered incubation to avoid double-counting birds that may have continued to nest in a new nest bowl after having their first nest destroyed (but see estimate of egg-laying failure below). Further, previous estimates of the number of geese nesting at Egg River were also based on incubating geese (see Kerbes et al. 1999 and references therein), so our data were comparable to those of previous studies. We assumed that nests with fresh down, but no eggs, had entered incubation, but failed before we found them (see Johnson and Shaffer 1990). We included 6, 2, 14, and 10 nests that had failed before we found them in each year, respectively, which corresponded to 0.3–4.4% of the sample size.

We defined the colony as the area where geese nested within 200 m of sample plots and determined the boundary of the colony for each year by using information

from sample plots and travels through the colony. We used a geographic information system (GIS) (Intera Tydac 1991) to determine colony size in each year. We excluded small lakes and riverbeds from the total area, as these were not used by nesting geese. We stratified the colony into a high-density stratum and a low-density stratum each year, again using information from sample plots and travels through the colony, and we used the GIS to estimate the area of each stratum. We used 35 nests/ha as the cut-off point between high and low density, which was close to the average nesting density in all years (see section 4.1.1 below).

We estimated the number of geese that failed during egg laying (ELF) from our estimates of the number of geese entering incubation (NGI) and daily survival rate during egg laying (DSR; see section 3.1.4 below) by the equation [$ELF = (NGI / DSR^{exposure}) - NGI$], where exposure was calculated by [(clutch size − 1) × 33/24 days]. This estimate may include some double-counting of geese that continued to nest in a new nest bowl after having their first nest destroyed (see Cooke et al. 1995). We suggest that potential bias associated with missing nests that had failed before we could detect them was low, because the detection probability of nests ranged between 0.83 and 1.0 during egg laying (Samelius and Alisauskas, unpubl. data). We estimated the confidence interval for the number of geese that failed during egg laying by using the upper and lower confidence limits of both the number of nesting geese and daily survival rate in the above formula.

3.1.3 Clutch size and drop-eggs

We defined clutch size as the number of eggs present in a nest at the start of incubation and included only data from initiation plots in our estimates of clutch size (n = 832 clutches from 4 years). Nests that were never incubated were excluded from the calculation of clutch size to avoid the inclusion of incomplete clutches. Geese occasionally laid eggs outside nest bowls (called drop-eggs hereafter), and we monitored drop-eggs at 10, 11, 19, and 19 initiation plots in 1995–1998, respectively. We calculated the rate of egg dropping for each year by dividing the number of drop-eggs by the number of nests initiated on the sample plots where egg dropping was monitored. This was a minimum estimate of egg dropping, as foxes and gulls scavenged these eggs quickly (Samelius and Alisauskas 1999, 2000). We examined the annual variation in rate of egg dropping by performing a chi-squared test on the number of drop-eggs relative to the number of nests initiated on the sample plots monitored for drop-eggs in each year (n = 101 drop-eggs from 4 years; PROC FREQ, SAS Institute Inc. 1990).

3.1.4 Nesting success

We used the Mayfield (1961, 1975) method to estimate nesting success during egg laying, incubation, and the whole nesting period (where the latter was the product of nesting success during both egg laying and incubation). We calculated confidence intervals for Mayfield (1961, 1975) estimates by following Johnson (1979) and used only data from initiation plots for calculations of nesting success (n = 934 nests from 4 years). Our estimate of nesting success during egg laying should be used with caution, because it is unknown whether Lesser Snow Geese continue to lay eggs in different nests if they fail early during egg laying (see Cooke et al. 1995).

3.1.5 Causes of nesting failure

The cause of nesting failure was determined at 13 initiation plots in 1995 and 11 initiation plots in 1996–1998. Nesting failure resulted from abandonment, nest depredation, mortality of incubating females, and flooding. However, abandonment and nest depredation could not be separated for most nests, because it was unknown if missing eggs were depredated or scavenged after nests were abandoned. We therefore used known abandonment (determined by the presence of cold eggs) as an index of the minimum proportion of nesting failure caused by abandonment (see Cooke et al. 1995).

3.1.6 Adult nesting mortality

We estimated adult nesting mortality both as the number of geese that died during nesting and as a proportion of nesting geese. We estimated the number of dead geese by multiplying the density of dead geese at sample plots by the area used by nesting geese following Thompson (1992). The proportion of geese that died during nesting in each year was calculated by dividing estimates of the number of dead geese by estimates of the number of nesting geese (see section 3.1.2 above). Long bones (i.e., femurs) from dead geese were collected and analyzed for avian cholera in all years (n = 103 long bones from 4 years). Analyses were performed by the National Wildlife Health Center in Madison, Wisconsin, in 1995 and 1996 (see Samuel et al. 1999) and by the Canadian Cooperative Wildlife Health Centre in Saskatoon, Saskatchewan, in 1997 and 1998.

We examined the chronology of nesting mortality by plotting the cumulative number of dead geese at initiation plots against nesting stage for each year from 1996 to 1998 (n = 38 dead geese from 19 sample plots and 3 years). Data from 1995 were not included, as nesting mortality was not monitored accurately that year (see section 3.1.1 above).

3.1.7 Hatch

We avoided travelling in the colony during hatch, as disturbance at this period can cause geese to abandon the last hatchlings (Cooke et al. 1995). Instead, we assumed that hatch occurred 23 days after the onset of incubation (Bousfield and Syroechkovskiy 1985; Cooke et al. 1995).

3.1.8 Brood size at hatch

We estimated brood size at hatch by monitoring the number of goslings in broods leaving the colony (see McEwen 1958). This was done by observing broods with spotting scopes (15–45×) from hills surrounding the colony (n = 1961 broods from 4 years). We observed broods leaving

the colony on 30 June to 3 July in 1995, 28 June to 1 July in 1996, 1–5 July in 1997, and 22–25 June in 1998.

3.1.9 Abundance of arctic foxes and other predators

We used the ratio of the number of foxes seen during nest surveys and the distance travelled during these surveys as an index of fox abundance for each year. Nest surveys were done at similar times of the day among years, and data included in calculating indices of fox abundance were limited to the nesting period by geese to avoid different detectability of foxes during goose presence and absence. Multiple observations of the same fox during one day were combined as one observation (individual foxes were identified by pelt patterns that were changing from winter to summer fur). We tested for annual variation in fox abundance by performing a chi-squared test in which data were arranged by the number of fox sightings per year and the expected number of fox sightings in each year corrected for sampling effort (i.e., expected number of fox sightings = proportion of total distance travelled × total number of foxes seen) following Neu et al. (1974) (n = 179 foxes from 4 years).

Glaucous Gulls were the other main predator of eggs at Egg River, and we used the number of gulls nesting in the colony as an index of gull abundance. Gull nests were found exclusively on islands of small lakes, and gulls nested in the same nest bowls among years (however, these were not necessarily the same birds among years). Nesting gulls were conspicuous, and we covered the colony systematically in a 1-km grid; we therefore suggest that the count of gull nests corresponded closely to the number of gulls nesting at Egg River. We may, however, have missed some nests in 1995 and 1996 before we learned in which lakes gulls nested.

3.1.10 Lemming abundance

We monitored small mammal abundance by running two transects of snap-traps in early July following Krebs and Wingate (1985). Trap-lines were located about 1 km outside the colony on dry slopes dominated by mountain avens *Dryas integrifolia* and arctic willow *Salix arctica*. We tested for annual variation in lemming abundance by performing a log-likelihood ratio test (Zar 1999) in which data were arranged by the number of lemmings trapped per year and the expected number of lemming captures in each year was corrected for sampling effort (i.e., expected number of lemming captures = proportion of total number of trap-nights × total number of lemming captures) following Neu et al. (1974) (n = 16 lemmings from 4 years).

3.2 Brood-rearing ecology

3.2.1 Goose distribution during brood rearing (aerial survey)

We monitored the distribution of geese during brood rearing by performing an aerial survey 2–3 weeks after hatch in each year. Our sampling frame included all of Banks Island Migratory Bird Sanctuary No. 1 (except for a narrow strip south of Kellett River), and we stratified the area into river valleys and uplands (we did not sample the uplands in 1995; Fig. 1). We calculated the area for each stratum using a GIS (Intera Tydac 1991; see Appendix 1 for the area of each stratum). Aerial surveys were conducted on 11–12 July in 1995, 9–11 July in 1996, 18–21 July in 1997, and 12–15 July in 1998, using a Bell 206 helicopter for 20–25 hours of flying time per year.

In each survey stratum, we randomly selected sample plots of 2 × 2 km and counted the number of geese by photographing all flocks of geese within each sample plot (see Reed and Chagnon 1987). We assumed that the detection probability of geese was close to 1.0, as >99% of the geese were white phase (see section 4.2.3 below) and contrasted well against the background. We used the same sampling scheme in all years, but the number of plots varied among years as a result of helicopter logistics (n = 98, 87, 99, and 78 plots in each year, respectively). We estimated the number of birds for each stratum following Thompson (1992). Three sample plots were excluded from the uplands in 1997, as they were not considered to be representative of the area (two plots were in the river valley of Adam River — a river system too small to form its own stratum — and one was too close to Big River).

Over 90% of Lesser Snow Geese nesting on Banks Island nest at Egg River (Kerbes et al. 1999), so additional geese encountered during the aerial survey were therefore predominantly nonbreeding geese (i.e., subadult geese or adults that did not breed in that year). We used the ratio of the number of geese nesting at Egg River and the number of geese encountered in the brood-rearing areas during the aerial survey as an index of breeding propensity in each year. This index should be used with caution, as the aerial survey may not have included all areas that geese use during the brood-rearing season (e.g., Barry [1960] found failed and nonbreeding geese at the Thomsen River at the northern end of the island) and may therefore be biased high.

3.2.2 Index of gosling survival

We used the ratio of the population of goslings found during the aerial survey and the population of goslings estimated to have left the colony as an index of gosling survival in 1996–1998 (the brood-rearing areas were only partially covered in 1995). Few broods were encountered at the perimeter of the bird sanctuary, and we suggest that few broods dispersed outside the area covered (see section 4.2.1 below). The population of goslings leaving the colony was estimated by multiplying brood size at hatch by the number of nesting pairs and nesting success during the incubation period. We estimated the confidence interval of gosling survival using the maximum and minimum number of goslings found during the aerial survey and the maximum and minimum number of goslings leaving the colony.

3.3 Population growth rate

We calculated annual growth rate, λ, for the nesting population at Egg River from 1953 to 1998 by performing a linear regression on ln values of population estimates following Eberhardt and Simmons (1992) (n = 10 population

estimates, where data from 1953 to 1995 were from Kerbes et al. [1999] and references therein; PROC GLM, SAS Institute Inc. 1990). Similarly, we also calculated the annual rate of change in population size (i.e., the proportional change in population size between years) for both the nesting population in 1995–1998 and the adult population in the brood-rearing areas in 1996–1998 (we were not able to estimate the population size in 1995) by dividing the population estimate from one year by that of the previous year following Alisauskas and Rockwell (2001). We calculated the variance for annual rate of change in population size by $[(\text{var}(N_{t+1})/N_t^2) + ((N_{t+1}^2 \times \text{var}(N_t))/N_t^4)]$, where N_t = population size in year 1 and N_{t+1} = population size in year 2 (see Doherty et al. 2002). We used average degrees of freedom for N_t and N_{t+1} as the sample size for calculations of the annual rate of change in population size.

3.4 Impact of grazing

3.4.1 Plant cover at Egg River

We examined plant cover at the Egg River colony by sampling the vegetation cover of all nest sample plots inside the colony in 1998 (i.e., all plots with geese nesting within 200 m were included). Vegetation cover was sampled from line transects extending from the centre of each sample plot and 30 m north. At every metre, we classified cover as plant or exposed soil. We inventoried plant cover from 29 June to 1 July, which was 7–9 days after the peak hatch of geese and 30–32 days after the first flowering of purple saxifrage *Saxifraga oppositifolia* (used as an indicator plant for spring phenology). We analyzed the relationship between nesting density and plant cover by performing linear regression on vegetation cover and cover by marsh ragwort *Senecio congestus* (an indicator of overgrazing; Jefferies and Abraham 1994) relative to the density of nesting geese (n = 2200 samples from 74 plots; PROC GLM, SAS Institute Inc. 1990). We corrected $\alpha = 0.05/2 = 0.025$, as the same data were used in two separate analyses.

3.4.2 Goose use and availability of graminoid plants in the brood-rearing areas

We examined the relation between goose use and availability of graminoid plants (i.e., grasses and sedges, families Gramineae and Cyperaceae, respectively) in the brood-rearing areas by collecting goose droppings and vegetation samples from river valleys and uplands of Banks Island Migratory Bird Sanctuary No. 1 in 1998. We focused our sampling on wet margins of ponds and lakes (called lake margins hereafter), as this appeared to be where geese concentrated foraging during aerial surveys in 1995–1997 and where geese in other areas of the Arctic concentrate their foraging (Giroux et al. 1984; Hughes et al. 1994). Sample sites, five in each of Big River, Storkerson River, Bernard River, and the uplands, were randomly selected from the sample scheme for the aerial survey (see section 3.2.1 above). We standardized sample sites as gently sloping margins of the pond or lake closest to the southwest corner of selected sample plots (lake margins were generally 3–5 m wide). At each site, we collected three samples of goose droppings (all droppings within 1 m^2 for each sample) and took three core samples of vegetation (84 mm in diameter) following the procedures of Jefferies and Abraham (1994). Samples were taken in the centre of each patch and 10 m to each side of the centre. For smaller patches (<40 m long), the centres of each patch and each quarter were sampled. We used average dry weight of droppings and graminoid plants from each site as the sampling unit in analyses.

In addition to vegetation and goose droppings collected at lake margins, we also sampled vegetation and goose droppings at snowpatch fens to examine differential use by geese and differences in availability of graminoid plants between habitats. Snowpatch fens were defined as distinct patches of vegetation located at lower parts of gently sloping hills (for more detail, see National Wetlands Working Group 1988). Logistic constraints limited our sampling of snowpatch fens to Big River. We matched sample sites for snowpatch fens with sample sites of ponds and lakes by selecting the fen closest to the sample site for lake margins. Snowpatch fens were sampled using the same procedures as for lake margins (see above).

Vegetation samples were processed within 24 hours of collection following procedures in Jefferies and Abraham (1994). We cut vegetation at soil or moss level and sorted vegetation to dead material, live graminoid plants, or live plants other than graminoids. We classified graminoid plants that had both live and dead parts as *live* if more than half the plant was green and *dead* if more than half the plant was brown. Dead graminoid plants were rare, and we included only live graminoid plants in this study. Vegetation samples and goose droppings were dried in the field, then redried to constant mass at 70°C in the laboratory and weighed (±0.001 g for vegetation and ±0.01 g for goose droppings).

We examined how the availability of graminoid plants varied among river valleys and relative to goose use by performing an ANCOVA on mass of graminoid plants against location and mass of goose droppings (n = 20 sites from four areas; PROC GLM, SAS Institute Inc. 1990). Data were nonlinear, so we square root-transformed the mass of both graminoid plants and goose droppings, as this provided the best linear approximation. We derived five candidate models on variation in abundance of graminoid plants that ranged from no variation among river valleys and no influence by goose use (i.e., variation around the grand mean) to include variation among river valleys, influence by goose use, and an interaction among river valleys and goose use. We used Akaike's information criterion (AIC) with small-sample adjustment (AICc) to select the candidate model that best explained the availability of graminoid plants at lake margins (Burnham and Anderson 1998). We selected the model with the lowest AICc value as the best model and considered models within 2 AICc units to be of similar quality (Burnham and Anderson 1998).

We examined if geese used lake margins and snowpatch fens differently by performing a paired t-test on differences in availability of goose droppings of matched samples from lake margins and snowpatch fens (n = 5 matched samples; PROC MEANS, SAS Institute Inc. 1990). Similarly, we examined if the availability of graminoid plants varied between habitats by performing a

paired *t*-test on differences in availability of graminoid plants of matched samples from lake margins and snowpatch fens (n = 5 matched samples; PROC MEANS, SAS Institute Inc. 1990).

3.5 Body condition of geese

We collected 25 Lesser Snow Geese upon arrival at Banks Island in both 1997 and 1998 to examine body condition of geese nesting on Banks Island. Geese were collected during the annual spring hunt at Sachs Harbour between 20 and 22 May in 1997 and 17 and 21 May in 1998. We used abdominal fat and protein index (sum of mass of breast muscles, leg muscles, and gizzard) as measures of body condition. We compared body condition of Lesser Snow Geese from Banks Island with that of Lesser Snow Geese from Karrak Lake, Nunavut, by performing ANOVAs on absolute differences in abdominal fat and protein index and ANCOVAs on differences corrected for structural size (called relative difference hereafter) by including PC1 component derived from principal component analysis (PROC PRINCOMP, SAS Institute Inc. 1990) on tarsus length, keel length, skull length, skull width, cranial height, culmen, and wing chord (n = 18 adult females from Banks Island and 43–45 adult females from Karrak Lake; PROC GLM, SAS Institute Inc. 1990).

3.6 Precision of estimates

We report 95% confidence intervals (CI) of estimates throughout this report unless otherwise stated.

4. Results

4.1 Nesting ecology

4.1.1 Number of nesting geese and area covered by nesting geese

The number of geese nesting at Egg River varied considerably among years, and we estimated that 264 000–452 000 Lesser Snow Geese nested at the colony in 1995–1998 (Table 1, Fig. 2). The number of nesting geese was negatively related to timing of snowmelt and was particularly low in 1997, when nesting was delayed by a very late snowmelt (snowmelt was late in 1995 as well, but less so than in 1997; Fig. 3). We have included Kerbes et al.'s (1999) estimate of 431 000 geese nesting at Egg River in 1995 for comparison (see Table 1 and Fig. 2). This estimate was based on aerial photographs obtained on 11 June 1995 (Kerbes et al. 1999). The number of geese failing during egg laying varied among years and appeared to be negatively related to timing of snowmelt; we estimated that 91 000 (95% CI = 39 000–189 000), 34 000 (95% CI = 6000–74 000), 127 000 (95% CI = 62 000–241 000), and 75 000 (95% CI = 36 000–126 000) Lesser Snow Geese failed during egg laying in 1995–1998, respectively.

The detection probability of nests ranged between 0.50 and 1.00 (Table 2). However, we suspect that the detection probability in 1995 may have been biased by the deployment of plot markers in that year (i.e., we may have been influenced by the nesting distribution of geese when selecting the exact location of plot markers). The annual detection probability of nests ranged between 0.79 and 1.00 in years after plot markers were deployed (mean = 0.93).

The area used by nesting geese (i.e., colony size) varied considerably among years and was 76.5, 87.2, 33.1, and 74.6 km^2 in each year, respectively (Fig. 4). Average nesting density was less variable among years, with means of 30 (95% CI = 23–39), 29 (95% CI = 25–33), 43 (95% CI = 32–59), and 35 (95% CI = 31–39) nests/ha in each year, respectively.

4.1.2 Spring and nesting chronology

The timing of snowmelt varied by about 19 days among years in 1995–1998, with 50% snow cover at about 3 June, 25 May, 8 June, and 20 May in each year, respectively (Table 3). Similarly, the breakup of Big River

Table 1
Number of Lesser Snow Geese nesting at Egg River in 1995–1998[a]

Year	Number of nesting geese (95% CI)[b]	Coefficient of variation	Sample size (number of nest plots)
1995	404 000 (313 000–522 000)	12.9	75
1996	436 000 (379 000–502 000)	7.1	87
1997	264 000 (194 000–359 000)	15.3	33
1998	452 000 (403 000–507 000)	5.7	72
Kerbes et al.'s (1999) estimate for 1995[c]	431 000 ± 48 000		

[a] Nesting was delayed by about 1 week in 1995 and 1997 compared with 1996 and 1998 (see Table 3).
[b] We estimated the number of nesting geese by using Program Distance (Thomas et al. 2002), and we stratified the colony based on information from sample plots and travels through the colony.
[c] This estimate was based on aerial photography obtained on 11 June 1995.

Table 2
Detection probability of Lesser Snow Goose nests at Egg River in 1995–1998[a]

Year	Stratum[b]	Detection probability (95% CI)	Nesting density (nests/ha) (95% CI)
1995	High density	0.75 (0.63–0.88)	75 (54–105)
	Low density	0.50 (0.38–0.65)	14 (10–21)
1996	High density	1.00 (n/a)	51 (45–57)
	Low density	0.79 (0.61–1.00)	18 (13–24)
1997	High density	0.80 (0.64–1.00)	98 (70–138)
	Low density	1.00 (n/a)	8 (5–14)
1998	High density	1.00 (n/a)	68 (59–78)
	Low density	1.00 (n/a)	15 (12–19)

[a] Detection probability in 1995 may have been biased by the deployment of plot markers in that year (i.e., we may have been influenced by the nesting distribution of geese when selecting the exact location of plot markers).
[b] We used 35 nests/ha as the cut-off point between high- and low-density areas.

Figure 2
Number of Lesser Snow Geese nesting at Egg River from 1953 to 1998 (data from 1953 to 1995 are from Kerbes et al. 1999 and references therein). Note that nesting was delayed by about 1 week in 1995 and 1997 compared with 1996 and 1998. Annual growth rate for the nesting population at Egg River was 4.2% from 1953 to 1998.

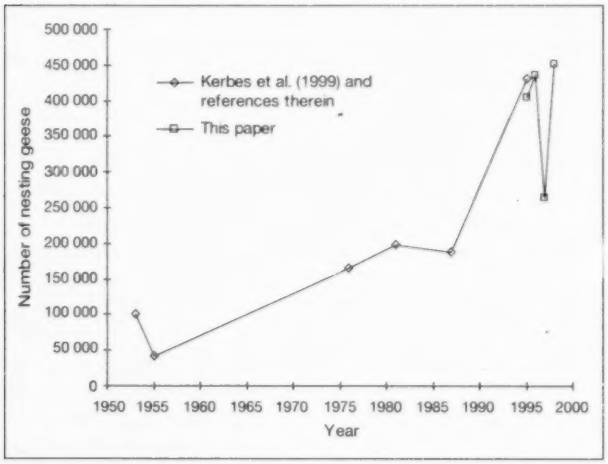
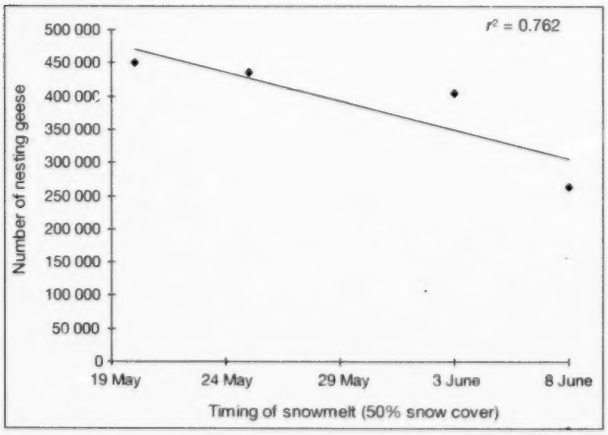


Figure 3
Correlation between timing of snowmelt and number of nesting geese at Egg River in 1995–1998



and the first flowering of purple saxifrage varied by about 15–17 days among years during the study (Table 3). Nesting chronology varied by about 10 days among years, with median nest initiation on 2 June, 1 June, 5 June, and 26 May in each year, respectively (Table 3, Fig. 5). Nest initiation was very synchronized within years, with 74% of geese initiating nests between 31 May and 4 June in 1995, 84% between 30 May and 3 June in 1996, 70% between 3 and 7 June in 1997, and 84% between 24 and 28 May in 1998.

Geese arrived at Banks Island in mid-May in 1995 (T. Lucas, Sachs Harbour, pers. commun.), but did not start to nest until about 2 weeks later due to snow cover (Samelius, pers. obs., Table 3). Few geese arrived at Banks Island before 24 May in 1996, and geese started to nest within a week of arrival on the breeding grounds, as most snow had melted before the arrival of geese (Samelius, pers. obs.). In 1997, geese arrived at Banks Island in mid-May (P. Raddi, Sachs Harbour, pers. commun.), but did not start to nest until about 2–3 weeks later due to snow cover (Samelius, pers. obs.). Geese arrived at Banks Island in mid-May in 1998 (T. Lucas, Sachs Harbour, pers. commun.), but did not start to nest until about 1 week later due to snow cover (Samelius, pers. obs.). Arrival dates at Banks Island during this study were similar to those reported in 1953 by Höhn (1954) and in 1955 by McEwen (1958).

4.1.3 Clutch size and drop-eggs

Clutch size ranged between 3.5 and 3.8 eggs in 1995–1998 and was lower in years when nesting was delayed by late snowmelt (Table 4, Fig. 6). Clutch size was comparable to that recorded at Egg River in 1955 and that recorded for Lesser Snow Geese at Wrangel Island, Russia, and Karrak Lake, Nunavut, but was slightly lower than that recorded for Lesser Snow Geese at La Pérouse Bay, Manitoba (McEwen 1958; Bousfield and Syroechkovskiy 1985; Cooke et al. 1995; Alisauskas, unpubl. data).

Geese dropped eggs outside of nest bowls at different rates among years ($\chi^2_{(3)} = 52.78$, $P < 0.001$), with a higher rate of egg dropping in 1995 and 1997, when nesting was delayed by late snowmelt (Fig. 7). We found 0.17, 0.03, 0.32, and 0.06 drop-eggs per initiated nest in each year, respectively (Table 5).

Figure 4
Geographic extent of the Egg River colony on Banks Island in 1995–1998, showing high and low nest densities. The extent of the colony and strata were determined from sample plots and travels through the colony.

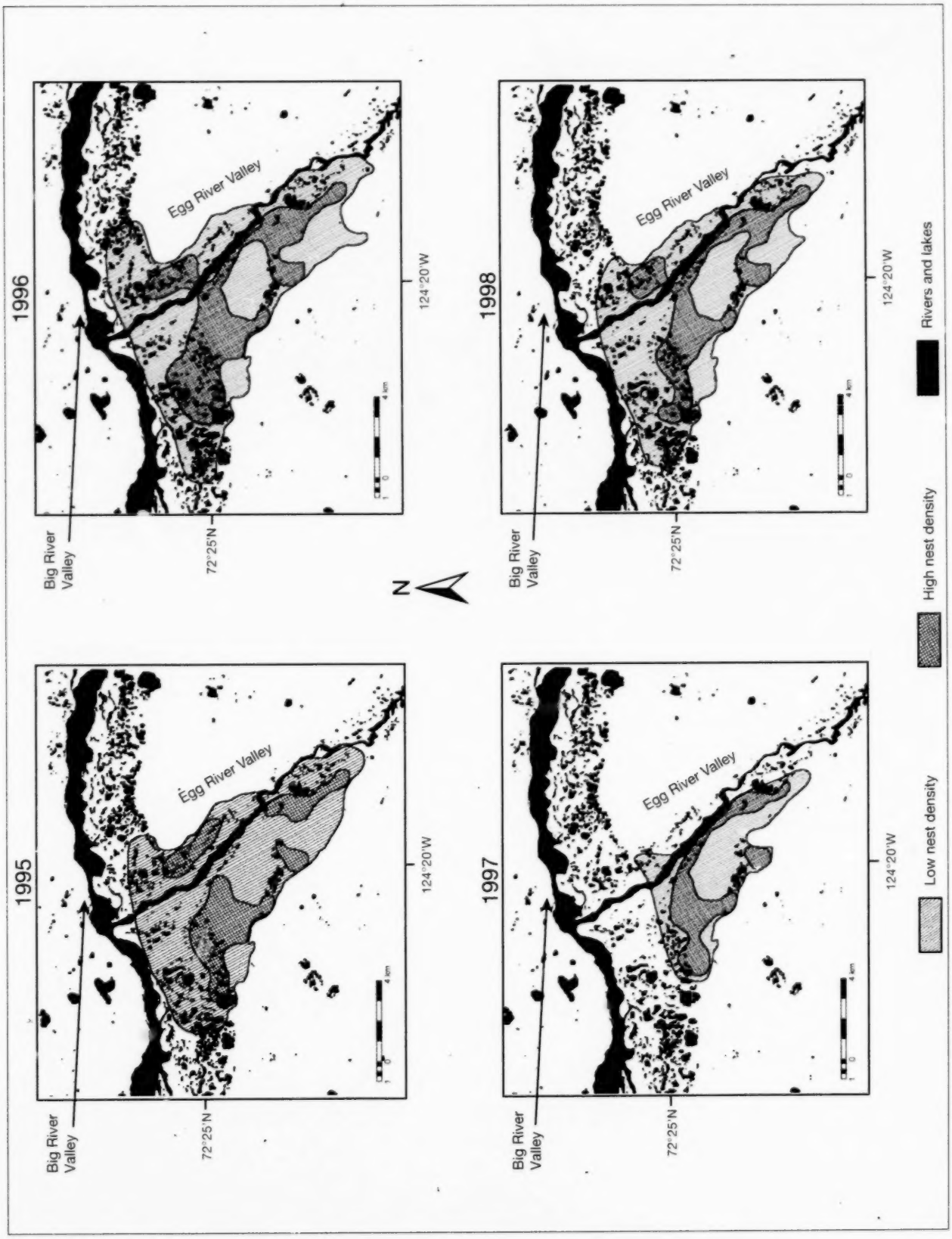


Table 3
Spring and nesting chronology at Egg River in 1995–1998

	Spring chronology			Nesting chronology	
Year	50% snow cover	Breakup of Big River	First flowering purple saxifrage	Median nest initiation	Time from arrival to start of nest initiation
1995	3 June	5 June	8 June	2 June	~2 weeks
1996	25 May	25 May	31 May	1 June	~1 week
1997	8 June	12 June	14 June	5 June	~2–3 weeks
1998	20 May	26 May	30 May	26 May	~1 week

Figure 5
Distribution of nest initiation dates at Egg River in 1995–1998. Nesting phenology varied by 10 days among years (median initiation was 26 May in 1998 and 5 June in 1997).

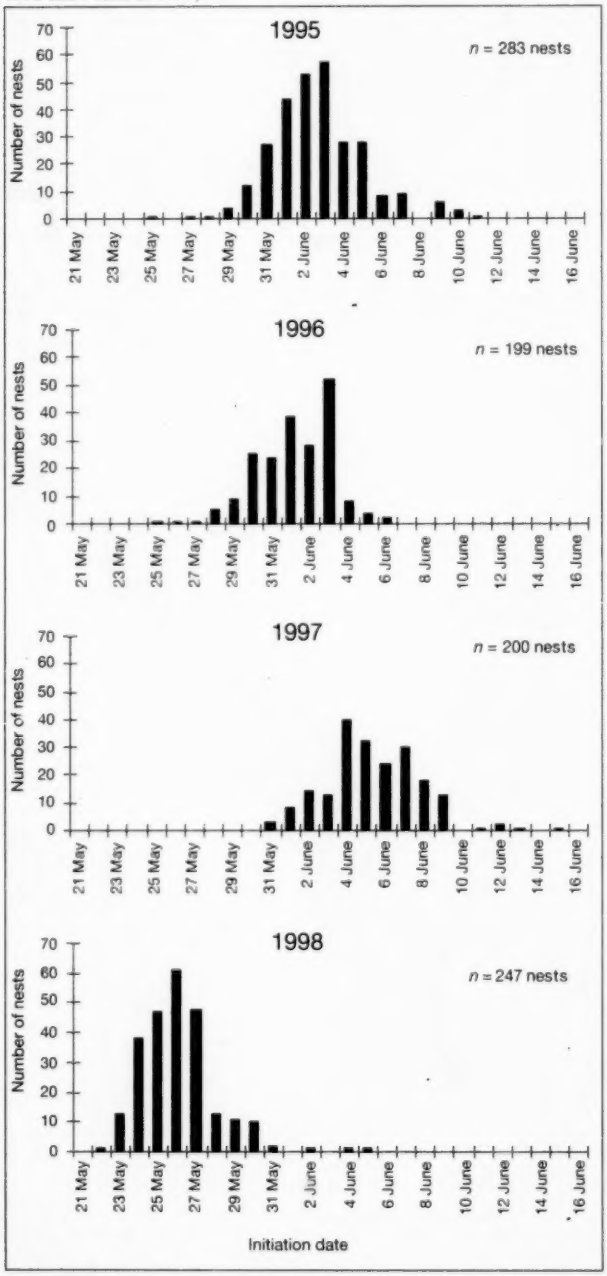


Table 4
Clutch size at Egg River in 1995–1998[a]

Colony	Year	Mean clutch size ± 95% CI	Sample size (number of nests)
Egg River	1995	3.5 ± 0.15	262
Egg River	1996	3.7 ± 0.12	194
Egg River	1997	3.7 ± 0.20	150
Egg River	1998	3.8 ± 0.12	226
Egg River[b]	1955	3.9	
Wrangel Island, Russia[c]	not specified	3.7	
Karrak Lake, Nunavut[d]	1991–2001	3.6[f]	
La Pérouse Bay, Manitoba[e]	1973–1991	4.2[g]	

[a] Nesting was delayed about 1 week longer in 1995 and 1997 than it was in 1996 and 1998 (see Table 3).
[b] McEwen (1958).
[c] Bousfield and Syroechkovskiy (1985).
[d] Alisauskas (unpubl. data).
[e] Cooke et al. (1995).
[f] Mean clutch size ranged from 3.5 to 3.8 eggs per clutch at Karrak Lake.
[g] Mean clutch size ranged from 3.6 to 4.8 eggs per clutch at La Pérouse Bay.

Figure 6
Correlation between timing of snowmelt and clutch size at Egg River in 1995–1998

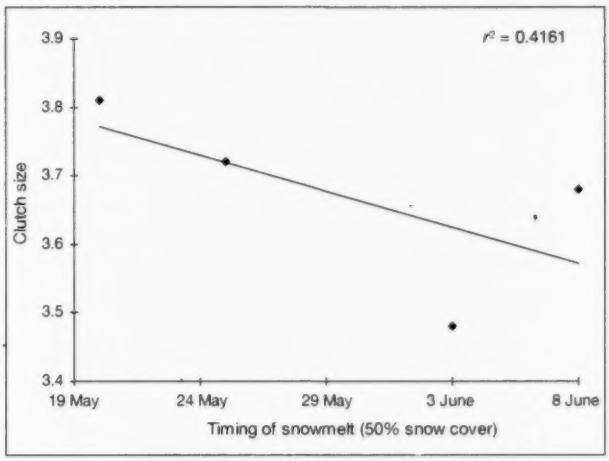


Figure 7
Correlation between timing of snowmelt and egg dropping at Egg River in 1995–1998

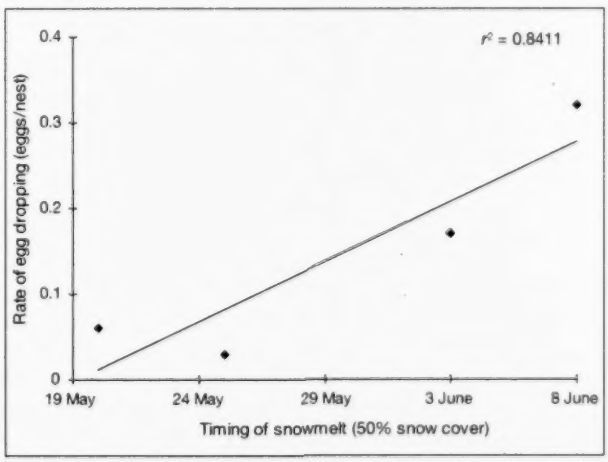


Table 5
Minimum rate of egg dropping at Egg River in 1995–1998[a]

Year	Number of drop-eggs per nest	Sample size (number of eggs)[b]
1995	0.17	17
1996	0.03	4
1997	0.32	65
1998	0.06	15

[a] Nesting was delayed by about 1 week in 1995 and 1997 compared with 1996 and 1998 (see Table 3).
[b] Egg dropping was monitored at 10, 11, 19, and 19 initiation plots in 1995–1998, respectively.

4.1.4 *Nesting success*

Nesting success for the whole nesting period ranged between 45% and 86% in 1995–1998 and was negatively related to timing of snowmelt (Table 6, Fig. 8). Incubation success at Egg River was comparable to that recorded at other large Lesser Snow Goose colonies, whereas it was generally higher than that recorded at Lesser Snow Goose colonies with fewer than 20000 nesting pairs (Bousfield and Syroechkovskiy 1985; Cooke et al. 1995; Armstrong 1998; Alisauskas, unpubl. data).

Daily nest survival varied by nesting period, among years, and to some extent within nesting period; it was lowest during egg laying in all years, was highest during early and mid incubation in all years, and dropped in late incubation in years with late snowmelt (Table 7, Fig. 9).

4.1.5 *Causes of nesting failure*

Failure of goose nests at Egg River was caused by abandonment, nest depredation, mortality of incubating females, and flooding of nests (Table 8). Failure caused by mortality of females was uncommon, and we observed only one female that was known to have died at the nest site (females may, however, have moved to other locations before dying, or dead females may have been removed by scavengers). Flooding of nests was also relatively uncommon and was observed only during egg laying in 1995 and 1997, causing 2% and 13% of observed nesting failures in these years, respectively. The minimum portion of nesting failure caused by abandonment ranged between 6% and 13% in 1995–1998. We could not differentiate between abandonment and depredation for 78–94% of nests because it was unknown whether missing eggs were depredated or scavenged after nests were abandoned (Table 8).

4.1.6 *Adult nesting mortality*

We estimated that 4300–8600 adult Lesser Snow Geese died at Egg River during nesting in 1996–1998 (Table 9). The estimate of 2200 adult geese dying at Egg River in 1995 is an estimate of the minimum number of dead geese, as dead birds were not accurately monitored in that year (i.e., only freshly dead birds were sampled). Nesting mortality appeared to be negatively related to timing of snowmelt, with more geese dying in the late year of 1997 than in the early years of 1996 and 1998. The number of dead birds corresponded to 1.0–3.3% of the nesting population in 1996–1998 (Table 9). We have included Samuel et al.'s (1999) estimates of 29300 and 19300 dead adult geese in 1995 and 1996, respectively, for comparison. The chronology of nesting mortality differed among years, with most geese dying during egg laying and early nesting in 1997 as compared with most geese dying in late incubation in 1996 and 1998 (Fig. 10).

The National Wildlife Health Center in Madison, Wisconsin, confirmed the presence of the bacterium responsible for avian cholera, *Pasteurella multocida*, in 12 of 38 and in 19 of 40 dead birds examined in 1995

Table 6
Nesting success at Egg River in 1995–1998[a]

Colony	Year	Success (%) ± 95% CI: Egg laying	Incubation	Nesting[b]	Sample size (number of nests)
Egg River	1995	83 ± 7	71 ± 9	59 ± 12	286
Egg River	1996	93 ± 5	93 ± 6	86 ± 11	199
Egg River	1997	70 ± 8	65 ± 13	45 ± 14	202
Egg River	1998	86 ± 6	88 ± 7	76 ± 11	247
Large colonies[c]					
Wrangel Island, Russia[d]	not specified		87[e]		
Karrak Lake, Nunavut[c]	1991–2001		81[f]		
Small colonies[c]					
Wrangel Island, Russia[d]	not specified		48[g]		
Anderson River, Northwest Territories[f]	1992–1993		45[h]		
La Pérouse Bay, Manitoba[g]	1973–1991		92[i]		

[a] Nesting was delayed by about 1 week in 1995 and 1997 compared with 1996 and 1998 (see Table 3).
[b] Nesting success for the whole nesting period is the product of nesting success during both egg laying and incubation.
[c] We defined large colonies as those with >20 000 nesting pairs and small colonies as those with <20 000 nesting pairs.
[d] Bousfield and Syroechkovskiy (1985).
[e] Alisauskas (unpubl. data).
[f] Armstrong (1998).
[g] Cooke et al. (1995).
[h] Incubation success ranged from 75% to 95% at Wrangel Island when the colony had >20000 nesting pairs.
[i] Incubation success ranged from 45% to 90% at Karrak Lake.
[j] Incubation success ranged from 0% to 78% at Wrangel Island when the colony had <20000 nesting pairs.
[k] Incubation success ranged from 5% to 85% at Anderson River.
[l] Incubation success ranged from 75% to 99% at La Pérouse Bay.

Figure 8
Correlation between timing of snowmelt and incubation success at Egg River in 1995–1998

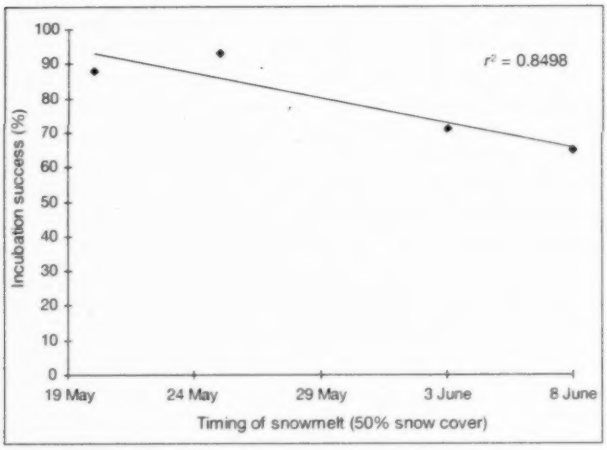


Table 7
Seasonal variation in nesting success at Egg River in 1995–1998[a]

	Mayfield daily survival rates ± 95% CI			
Year	Egg laying	Early incubation	Mid incubation	Late incubation
1995	0.948 ± 0.02	0.995 ± 0.003	0.993 ± 0.004	0.965 ± 0.010
1996	0.981 ± 0.02	0.999 ± 0.001	0.997 ± 0.003	0.994 ± 0.004
1997	0.906 ± 0.03	0.988 ± 0.006	0.985 ± 0.007	0.971 ± 0.012
1998	0.962 ± 0.02	0.996 ± 0.003	0.995 ± 0.003	0.992 ± 0.005

[a] Nesting was delayed by about 1 week in 1995 and 1997 compared with 1996 and 1998 (see Table 3).

and 1996, respectively (see Samuel et al. 1999). The Canadian Cooperative Wildlife Health Centre in Saskatoon, Saskatchewan, confirmed *P. multocida* in 4 of 15 and in 3 of 10 dead birds examined in 1997 and 1998, respectively. However, the proportion of geese that died from avian cholera may have been considerably higher, as detection of the bacterium causing avian cholera may have been reduced because analyses were done 1–2 months after the death of the birds (Samuel et al. 1999).

4.1.7 Hatch

Peak hatch was estimated as 30 June, 29 June, 2 July, and 22 June in 1995–1998, respectively. This corresponded well with observations of many eggs hatching on 28 and 29 June in 1995 and observations of many broods leaving the colony on 29 June to 1 July in 1996, 2–5 July in 1997, and 22–25 June in 1998. Weather conditions were cold and wet during early hatch in 1995, which kept geese on nests until 30 June, when conditions started to improve. Weather conditions were good throughout hatch in 1996. Weather conditions were mainly cloudy with fog and drizzling rain during hatch in 1997 (e.g., there was freezing rain overnight on 4 and 5 July in 1997). Weather conditions were mainly favourable during hatch in 1998, except for rain showers during the night of 24 June.

Figure 9
Relative survival of Lesser Snow Goose nests and predicted number of nesting geese at Egg River in 1995–1998. Predicted number of nesting geese was calculated from estimates of number of geese entering incubation and estimates of daily survival rates of nests. Egg laying is represented by negative incubation. Nesting was delayed by about 1 week in 1995 and 1997 compared with 1996 and 1998.

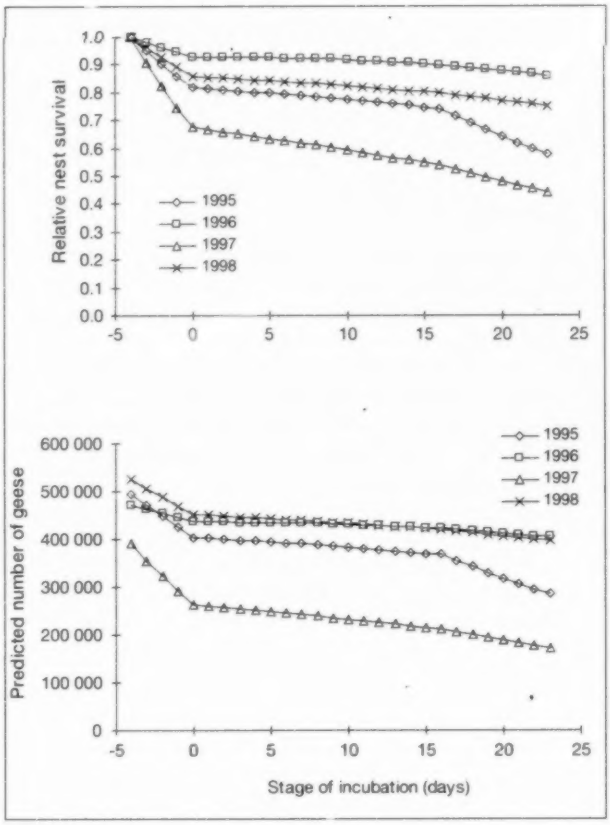


Table 8
Causes of nesting failure at Egg River in 1995–1998

Year	Abandonment (%)	Death of female (%)	Flooding[a] (%)	Abandonment or depredation[b] (%)	Sample size (number of nests)[c]
1995	13	2	2	83	46
1996	6	0	0	94	16
1997	9	0	13	78	23
1998	9	0	0	91	22

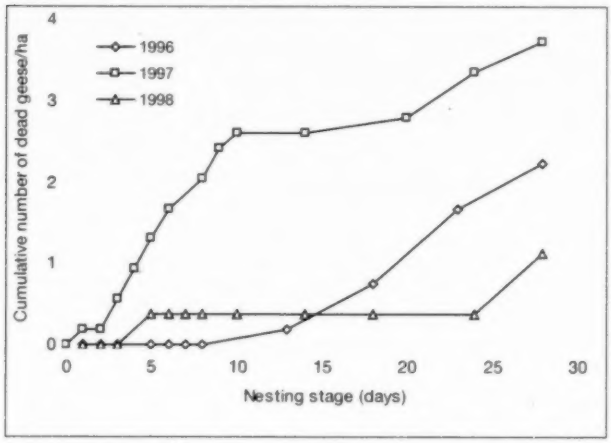
[a] Flooding of nests was caused by spring snowmelt.
[b] We could not separate abandonment from depredation for most nests because it was unknown if missing eggs were depredated or scavenged from abandoned nests.
[c] Cause of nesting failure was monitored at 13 initiation plots in 1995 and 11 initiation plots in 1996–1998.

Table 9
Nesting mortality of Lesser Snow Geese at Egg River in 1995–1998[a]

Year	Number of dead geese ± 95% CI	Proportion of dead geese (%)
1995[b]	2200 ± 1900	0.5
1996	6300 ± 6900	1.4
1997	8600 ± 4800	3.3
1998	4300 ± 2800	1.0
Samuel et al.'s (1999) estimate for 1995	29 300	7.3
Samuel et al.'s (1999) estimate for 1996	19 300	4.4

[a] Nesting was delayed by about 1 week in 1995 and 1997 compared with 1996 and 1998 (see Table 3).
[b] Only freshly dead birds were sampled in 1995, and our estimate of nesting mortality is therefore a minimum estimate of dead birds in that year (see section 3.1.1).

Figure 10
Cumulative number of dead Lesser Snow Geese at Egg River in 1996–1998 (number of dead geese was not monitored accurately in 1995 and was therefore not included). Egg laying includes the first 5 days of nesting, whereas incubation includes the last 23 days of nesting. Nesting was delayed by about 1 week in 1997 compared with 1996 and 1998.



4.1.8 Brood size at hatch

Brood size at hatch varied among years and ranged between 3.1 and 3.6 young in 1995–1998 (Table 10). The number of young per brood was negatively related to spring chronology and was lower in 1995 and 1997, when nesting was delayed by late snowmelt. Brood size at hatch was comparable to that recorded at Egg River in 1955 (McEwen 1958) and average brood size at hatch for Lesser Snow Geese at La Pérouse Bay, Manitoba (Cooke et al. 1995).

4.1.9 Abundance of arctic foxes and other predators

The abundance of arctic foxes varied among years, with more foxes frequenting the colony in 1997 and 1998 than in 1995 and 1996 ($\chi^2_{(3)} = 70.68$, $P < 0.001$; Fig. 11). We sighted 24 foxes during 430 km travelled ($n = 31$ days), 19 foxes during 400 km travelled ($n = 30$ days), 75 foxes during 329 km travelled ($n = 29$ days), and 61 foxes during 395 km travelled ($n = 32$ days) in each year, respectively. The peak in fox abundance followed 1 year after the peak in lemming abundance (Fig. 11). We saw no apparent relationship between fox abundance and goose numbers (either present or previous goose numbers).

The number of nesting Glaucous Gulls was similar or slightly increasing throughout the study. In total, we found 51, 64, 68, and 80 nests in each year, respectively. As discussed above, we might have missed some nests in 1995 and 1996, before we learned on which islands gulls nested.

In addition to arctic foxes and Glaucous Gulls, both Pomarine and Long-tailed jaegers frequented the colony in all years. We confirmed two breeding attempts by Long-tailed Jaegers in 1996 and one in 1997. We saw wolves near or within the colony twice in 1995 (two wolves on the first occasion and four on the second), and we saw two wolves about 1 km outside the colony in 1998. We saw no wolves at or near the colony in 1996 or 1997.

Human impact, in addition to that of our activities, was low in all years and limited by accessibility by snow machines; we saw 1–2 parties collecting eggs and geese in 1995, none in 1996, 5–10 in 1997, and 1 in 1998.

4.1.10 Lemming abundance

Lemming abundance varied among years, with peak abundance in 1996 and low numbers in other years ($G_{(3)} = 13.98$, $P < 0.005$). We captured 1 lemming in 360 trap-nights, 11 lemmings in 359 trap-nights, 2 lemmings in 360 trap-nights, and 2 lemmings in 360 trap-nights in each year, respectively. Lemming abundance at Egg River followed that recorded at other locations on Banks Island, but was of apparently lower magnitude (Dr. N. Larter, Department of Resources, Wildlife & Economic Development, Government of Northwest Territories, Fort Simpson, pers. commun.; see also Krebs et al. 2002).

4.2 Brood-rearing ecology

4.2.1 Goose distribution during brood rearing

We estimated that 503 000, 644 000, and 441 000 adult Lesser Snow Geese were distributed throughout Banks Island Migratory Bird Sanctuary No. 1 during the brood-rearing season in 1996–1998, respectively (Table 11, Fig. 12). This was similar to our estimate of the number of geese nesting at Egg River in 1996 and 1998, but was 380 000 more geese than we estimated were nesting at Egg River in the late year of 1997 (Table 1). Similarly, breeding propensity appeared to be negatively correlated with timing of snowmelt (Fig. 13), providing further evidence that late years were characterized by large numbers of nonbreeding geese. We estimated that 946 000 (± 100 000) adult geese were distributed throughout the sanctuary in 1997 when the three nonrepresentative plots were not excluded (i.e., 682 000 more adult geese than were estimated to nest at Egg River in that year).

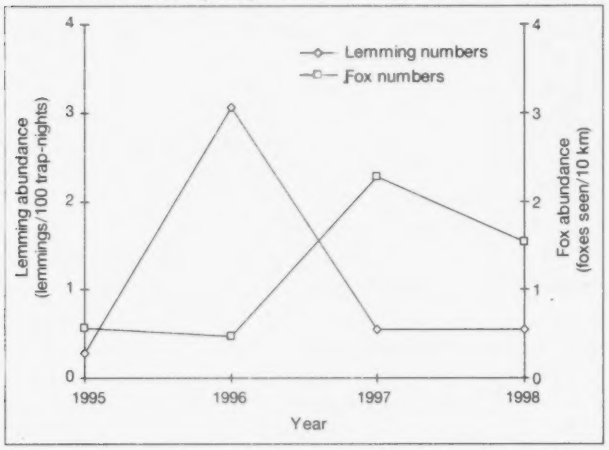
Successfully breeding geese (i.e., geese with young) were found closer to Egg River than failed and nonbreeding geese, with the highest densities of geese with young in the river valleys from Lennie River to Storkerson River (Table 12). Broods dispersed farther from the colony in 1996 and 1998 than in 1995 and 1997, with high densities

Table 10
Brood size at hatch at Egg River in 1995–1998[a]

Colony	Year	Brood size ± 95% CI	Sample size (number of broods)	Reduction during nesting (%)[b]
Egg River	1995	3.2 ± 0.12	554	9
Egg River	1996	3.6 ± 0.09	583	3
Egg River	1997	3.1 ± 0.14	395	16
Egg River	1998	3.5 ± 0.11	429	8
Egg River[c]	1955	3.3		15
La Pérouse Bay, Manitoba[d]	1973–1991	3.6[e]		14

[a] Nesting was delayed by about 1 week in 1995 and 1997 compared with 1996 and 1998 (see Table 3).
[b] Reduction during nesting was calculated as [(clutch size – brood size) / clutch size] × 100 (see Table 4 for clutch size).
[c] McEwen (1958).
[d] Cooke et al. (1995).
[e] Brood size at hatch ranged from 3.1 to 4.3 young per brood at La Pérouse Bay.

Figure 11
Abundance of lemmings and arctic foxes at Egg River in 1995–1998. Lemming abundance at Egg River followed cycles recorded at other locations on Banks Island, but was of apparently lower magnitude (N. Larter, Department of Resources, Wildlife & Economic Development, Government of Northwest Territories, Fort Simpson, pers. commun.; see also Krebs et al. 2002).



of breeding birds in the river valleys from Kellett River to Satchik River. In 1998, there were also high densities of breeding birds in the delta of Bernard River, approximately 125 km north of Egg River. The goslings that were found the farthest away from Egg River were found about 135 km from Egg River in both 1996 and 1998 (at the junction of the Egina and Bernard rivers). Even though the density of breeding geese was low on the uplands, its vast area (80% of the study area) resulted in the uplands containing the largest number of young and breeding geese in 1996–1998.

Failed and nonbreeding geese moved north and farther away from Egg River than geese with young, with the highest density of failed and nonbreeding birds found in the delta of Bernard River, about 125 km north of Egg River (Table 12). In 1995 and 1997, which were both late years with low nesting success, there were more failed and nonbreeding birds than there were breeding birds at the time of the aerial survey (Table 11). This was especially true in 1997, when there were high densities and numbers of failed and nonbreeding geese in the delta of Bernard River and the uplands.

4.2.2 Index of gosling survival

The population of goslings found during the aerial survey ranged between 27 and 44% of the population of goslings estimated to have left Egg River in 1996–1998 (Table 13); in other words, more than half of the goslings were estimated to have died during the first 2–3 weeks after hatch. Gosling survival at the age of 2–3 weeks on Banks Island was similar to that recorded for Lesser Snow Goose goslings at the age of 4–5 weeks at Karrak Lake, Nunavut, and La Pérouse Bay, Manitoba (Williams et al. 1993; Slattery 1994).

4.2.3 Proportion of blue geese

The percentage of blue geese was 0.36% (± 0.08%), 0.28% (± 0.09%), 0.26% (± 0.06%), and 0.47% (± 0.11%) of all adults encountered during the aerial survey in 1995–1998, respectively. We estimated that 0.33% (± 0.02%) of the adult geese encountered during the aerial survey were blue geese in all 4 years combined (n = 78 362 adult geese).

4.3 Population growth rate

Annual growth rate, λ, for the nesting population at Egg River was 1.042 (± 0.014) from 1953 to 1998 (r^2 = 0.85) and 1.045 (± 0.025) from 1976 to 1998 (r^2 = 0.75). This was lower than, and barely overlapping with, the annual growth rate of 1.109 (± 0.056) and 1.076 (± 0.058) for Ross' Geese *Chen rossii* and Lesser Snow Geese at Karrak Lake, Nunavut, respectively (Alisauskas 2001), and the annual growth rate of at least 5% for the mid-continental population of Lesser Snow Geese (Abraham and Jefferies 1997). The annual rate of change in population size of the nesting population ranged between 0.61 and 1.71 in 1995–1998, and the annual rate of change in population size for the adult population in the brood-rearing areas of Banks Island Migratory Bird Sanctuary No. 1 ranged between 0.68 and 1.29 in 1996–1998 (Table 14). Further, the annual rate of change in population size for the nesting population and the adult population in the brood-rearing areas showed opposite trends, and the magnitude of change in one parameter appeared to be unrelated to that of the other.

4.4 Impact of grazing

4.4.1 Plant cover at Egg River

There was 66.8% (± 2.0%) plant cover at the Egg River colony on 29 June to 1 July in 1998 (Appendix 2). Remaining parts of the colony were exposed soil and small bodies of water (<10 m wide and too small to show on a 1:50 000-scale map), covering 33.0% (± 2.0%) and 0.2% (± 0.2%) each. The most frequent plant groups and their cover were mountain avens (*Dryas* spp.), 21.5% (± 1.8%);

Table 11
Number of Lesser Snow Geese in the brood-rearing areas of Banks Island Migratory Bird Sanctuary No. 1 in 1995–1998[a,b]

Location	Number of geese ± 95% CI			
	1995	1996	1997	1998
Adult geese with goslings				
Kellett River	980 ± 2 100	2 030 ± 1 030	60 ± 120	3 980 ± 4 060
Lennie River	2 820 ± 1 990	3 240 ± 1 360	1 160 ± 780	2 080 ± 1 700
Big River and Sea Otter River	38 130 ± 6 740	28 180 ± 7 290	30 800 ± 8 930	29 000 ± 8 510
Storkerson River	18 720 ± 3 870	20 910 ± 7 170	14 920 ± 6 280	19 040 ± 6 790
Satchik River	630 ± 380	4 080 ± 1 280	190 ± 390	2 980 ± 2 320
Bernard River, delta	0 ± 0	970 ± 960	0 ± 0	17 380 ± 10 290
Bernard River, rest	no data	11 130 ± 8 140	6 130 ± 11 760	48 340 ± 28 330
Uplands	no data	226 900 ± 104 730	38 670 ± 60 370	165 600 ± 99 040
Total	incomplete data	297 420 ± 12 660	91 930 ± 16 120	288 390 ± 28 630
Goslings				
Kellett River	650 ± 1 300	2 010 ± 750	10 ± 20	1 760 ± 1 440
Lennie River	1 340 ± 730	2 750 ± 920	220 ± 190	1 470 ± 1 560
Big River and Sea Otter River	33 050 ± 4 470	28 960 ± 8 630	24 750 ± 7 550	27 450 ± 7 290
Storkerson River	18 050 ± 3 650	18 430 ± 3 770	7 890 ± 2 830	20 680 ± 6 860
Satchik River	430 ± 230	4 190 ± 1 130	10 ± 20	2 620 ± 1 840
Bernard River, delta	0 ± 0	730 ± 490	0 ± 0	11 370 ± 11 620
Bernard River, rest	no data	8 470 ± 5 780	820 ± 1 420	51 300 ± 24 610
Uplands	no data	246 520 ± 118 580	37 380 ± 59 080	183 240 ± 105 450
Total	incomplete data	312 060 ± 11 030	71 070 ± 8 600	299 890 ± 25 700
Failed and nonbreeding geese				
Kellett River	1 260 ± 2 660	100 ± 200	2 650 ± 4 580	70 ± 160
Lennie River	710 ± 900	40 ± 70	2 150 ± 2 010	240 ± 480
Big River and Sea Otter River	7 600 ± 4 330	5 550 ± 3 630	21 500 ± 14 970	8 670 ± 7 380
Storkerson River	12 560 ± 9 680	5 020 ± 5 140	37 670 ± 22 100	10 270 ± 9 250
Satchik River	3 020 ± 1 770	470 ± 630	4 660 ± 3 170	1 670 ± 1 810
Bernard River, delta	40 280 ± 28 300	26 720 ± 31 700	67 680 ± 57 990	25 840 ± 17 850
Bernard River, rest	no data	6 330 ± 11 180	59 550 ± 83 560	17 460 ± 35 830
Uplands	no data	161 270 ± 202 190	355 980 ± 641 090	88 010 ± 100 820
Total	incomplete data	205 500 ± 28 650	551 840 ± 99 390	152 230 ± 36 430
All adult geese				
Kellett River	2 240 ± 4 760	2 130 ± 980	2 710 ± 4 560	4 050 ± 4 070
Lennie River	3 530 ± 2 800	3 270 ± 1 360	3 310 ± 2 290	2 320 ± 1 980
Big River and Sea Otter River	45 730 ± 7 690	33 720 ± 8 000	52 300 ± 17 210	37 670 ± 10 530
Storkerson River	31 280 ± 11 990	25 920 ± 11 050	52 590 ± 20 350	29 300 ± 14 640
Satchik River	3 650 ± 1 800	4 550 ± 1 000	4 860 ± 3 040	4 650 ± 2 530
Bernard River, delta	40 280 ± 28 300	27 690 ± 31 160	67 680 ± 57 990	43 220 ± 9 150
Bernard River, rest	no data	17 460 ± 17 640	65 680 ± 83 930	65 800 ± 49 060
Uplands	no data	388 170 ± 264 000	394 640 ± 636 340	253 610 ± 144 160
Total	incomplete data	502 920 ± 33 160	643 770 ± 99 710	440 620 ± 47 090

[a] Uplands were not surveyed in 1995.
[b] Discrepancy between total number of geese and number of geese in each stratum is due to rounding of numbers.

Figure 12
Number of Lesser Snow Geese in the brood-rearing areas of Banks Island Migratory Bird Sanctuary No. 1 in 1996–1998 (uplands were not surveyed in 1995, so we were unable to estimate number of geese in that year). Nesting was delayed by about 1 week in 1997 compared with 1996 and 1998.

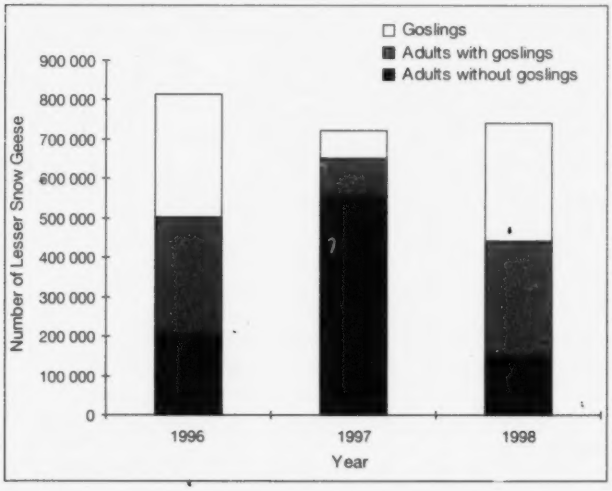
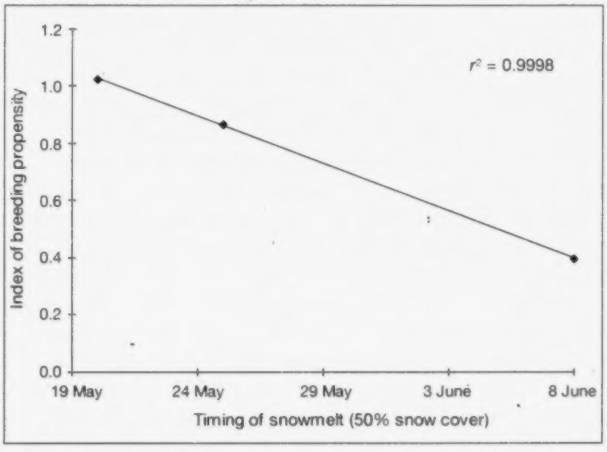


Figure 13
Correlation between timing of snowmelt and index of breeding propensity at Banks Island in 1996–1998. We used the ratio of number of geese nesting at Egg River and number of geese encountered in the brood-rearing areas as an index of breeding propensity. This index may be biased high, as the aerial survey may not have included all areas that geese use during the brood-rearing season (e.g., Barry [1960] found failed and nonbreeding geese at the Thomsen River at the northern part of the island).



mosses (phylum Bryophyta), 21.2% (± 1.8%); and willows (*Salix* spp.), 15.2% (± 1.6%). Graminoid plants (families Gramineae and Cyperaceae) had 3.8% (± 0.8%) coverage, whereas marsh ragwort *Senecio congestus* had 0.9% (± 0.4%) coverage.

Plant cover at the Egg River colony was negatively correlated with the density of nesting geese ($F_{(1,72)} = 6.22$, $P = 0.01$, $r^2 = 0.080$), whereas cover by marsh ragwort was positively correlated with the density of nesting geese ($F_{(1,72)} = 17.67$, $P < 0.001$, $r^2 = 0.20$).

4.4.2 *Goose use and availability of graminoid plants in the brood-rearing areas*

The availability of graminoid plants at lake margins ranged between 0.6 and 94.5 g/m^2 and was negatively related to goose use, as illustrated by the model that best described the availability of graminoid plants, including only goose droppings ($w_i = 0.99$, $r^2 = 0.53$; Table 15, Fig. 14). The availability of graminoid plants was similar among locations (i.e., Big River, Storkerson River, Bernard River, and the uplands), and the influence of goose use was similar among locations, as illustrated by models including location and an interaction between goose droppings and location being >2 AIC*c* units apart from the best model.

Lake margins and snowpatch fens in the Big River valley had a similar number of goose droppings ($t_{(4)} = 1.59$, $P = 0.19$) and a similar abundance of graminoid plants ($t_{(4)} = 1.45$, $P = 0.22$), illustrating that goose use and availability of graminoid plants were similar between habitats. There was, however, a trend for lake margins to have more goose droppings than snowpatch fens (11.5 ± 15.2 versus 2.0 ± 3.7 g/m^2, respectively), whereas the trend was reversed for the availability of graminoid plants (30.2 ± 22.3 versus 60.0 ± 32.1 g/m^2, respectively).

4.5 Body condition of geese

Adult female Lesser Snow Geese had, on average, 106 g (± 8.5 g) of abdominal fat and 699 g (± 37 g) of gizzard, breast, and leg muscles upon arrival at Banks Island ($n = 6$ females from 1997 and 12 females from 1998; Appendix 3). Adult female Lesser Snow Geese from Banks Island had similar amounts of absolute and relative (i.e., corrected for structural size) abdominal fat ($F_{\text{absolute fat}(3,60)} = 2.13$, $P = 0.15$, $F_{\text{relative fat}(6,55)} = 2.60$, $P = 0.11$) and muscle protein ($F_{\text{absolute protein}(3,59)} = 1.75$, $P = 0.19$, $F_{\text{relative protein}(6,54)} = 0.93$, $P = 0.34$) upon arrival at the breeding grounds as adult female Lesser Snow Geese from Karrak Lake, Nunavut. Adult female Lesser Snow Geese from Banks Island were structurally smaller than those from Karrak Lake ($F_{(1,60)} = 6.56$, $P = 0.01$).

Comparisons of body condition of geese collected at Egg River and Karrak Lake were, however, constrained by differences in the timing of collection; females collected at Karrak Lake had larger developing follicles upon collection than had females collected at Banks Island and had, thus, invested more in clutch formation than had females from Banks Island. Comparison of muscle protein may have been especially misleading, as females from Karrak Lake had 21.8 g more gizzard, breast, and leg muscle than females from Banks Island, even though they had invested more in clutch formation. Comparisons of abdominal fat were probably more representative, with females from Banks Island having 8.0 g more abdominal fat than females from Karrak Lake.

Table 12
Densities of Lesser Snow Geese in the brood-rearing areas of Banks Island Migratory Bird Sanctuary No. 1 in 1995–1998[a]

	Densities of geese (birds/km^2 ± 95% CI)			
Location	1995	1996	1997	1998
Adult geese with goslings				
Kellett River	11 ± 25	23 ± 14	1 ± 2	45 ± 53
Lennie River	49 ± 48	56 ± 33	20 ± 19	36 ± 38
Big River and Sea Otter River	41 ± 8	30 ± 8	33 ± 10	31 ± 10
Storkerson River	34 ± 8	38 ± 14	27 ± 12	35 ± 13
Satchik River	7 ± 6	48 ± 19	2 ± 6	35 ± 32
Bernard River, delta	0 ± 0	3 ± 4	0 ± 0	61 ± 38
Bernard River, rest	no data	7 ± 5	4 ± 7	30 ± 18
Uplands	no data	16 ± 7	3 ± 4	11 ± 7
Goslings				
Kellett River	7 ± 16	22 ± 10	0.1 ± 0.3	20 ± 19
Lennie River	23 ± 17	47 ± 22	4 ± 5	25 ± 35
Big River and Sea Otter River	36 ± 5	31 ± 10	27 ± 9	30 ± 8
Storkerson River	33 ± 7	34 ± 7	14 ± 6	38 ± 13
Satchik River	5 ± 4	50 ± 16	0.1 ± 0.3	31 ± 26
Bernard River, delta	0 ± 0	3 ± 2	0 ± 0	40 ± 43
Bernard River, rest	no data	5 ± 4	1 ± 1	31 ± 15
Uplands	no data	17 ± 8	3 ± 4	13 ± 7
Failed and nonbreeding geese				
Kellett River	14 ± 32	1 ± 3	30 ± 62	1 ± 2
Lennie River	12 ± 21	1 ± 2	37 ± 48	4 ± 11
Big River and Sea Otter River	8 ± 5	6 ± 4	23 ± 17	9 ± 8
Storkerson River	23 ± 19	9 ± 10	69 ± 43	19 ± 18
Satchik River	36 ± 28	6 ± 9	55 ± 46	20 ± 25
Bernard River, delta	142 ± 107	94 ± 117	239 ± 214	91 ± 66
Bernard River, rest	no data	4 ± 7	36 ± 52	11 ± 22
Uplands	no data	11 ± 14	25 ± 45	6 ± 7
All adult geese				
Kellett River	25 ± 57	24 ± 13	30 ± 62	45 ± 53
Lennie River	61 ± 67	56 ± 32	57 ± 55	40 ± 45
Big River and Sea Otter River	49 ± 9	36 ± 9	56 ± 20	41 ± 12
Storkerson River	57 ± 23	47 ± 21	96 ± 40	54 ± 28
Satchik River	43 ± 28	54 ± 15	58 ± 44	55 ± 35
Bernard River, delta	142 ± 107	98 ± 115	239 ± 214	153 ± 34
Bernard River, rest	no data	11 ± 11	40 ± 52	40 ± 30
Uplands	no data	27 ± 18	27 ± 44	18 ± 10

[a] Uplands were not surveyed in 1995.

Table 13
Index of gosling survival during the first 2–3 weeks after hatch for Lesser Snow Goose on Banks Island in 1996–1998[a]

Location	Year	Survival index (precision of estimate) (%)	Number of days after peak hatch
Egg River	1996	43 (33–56)	10–12
Egg River	1997	27 (14–52)	16–19
Egg River	1998	44 (31–60)	20–23
Karrak Lake, Nunavut[b]	1991–1992	33–50	~28
La Pérouse Bay, Manitoba[c]	1973–1991	35–65[d]	~35

[a] Brood-rearing areas were not completely surveyed in 1995, so we were not able to estimate gosling survival for that year.
[b] Slattery (1994).
[c] Williams et al. (1993).
[d] Gosling survival decreased from about 65% to about 35–40% as food abundance at La Pérouse Bay decreased (Williams et al. 1993)

We were unable to perform contaminant analysis of birds upon arrival at Banks Island, as this proved to be very expensive. However, Braune et al. (1999) found that contaminant levels of Lesser Snow Geese collected at Tuktoyaktuk in 1989 and Kendall Island in 1994 were low or below detection limits, as were contaminant levels of Arctic-nesting geese in general.

Table 14
Annual rate of change in population size (λ) for the nesting population of Lesser Snow Geese at Egg River and the adult population of Lesser Snow Geese in the brood-rearing areas of Banks Island Migratory Bird Sanctuary No. 1 in 1995–1998

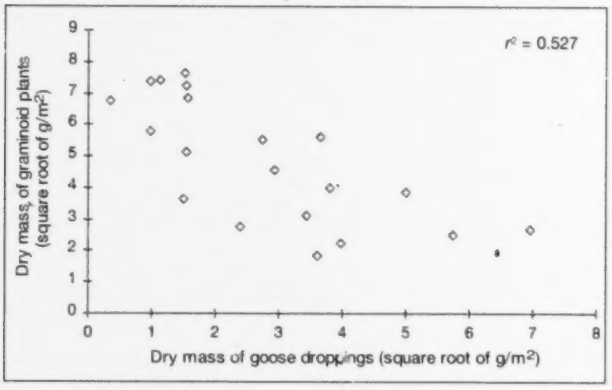
Years	λ for the nesting population ± 95% CI	λ for the brood-rearing population ± 95% CI
From 1995 to 1996	1.08 ± 0.31	no data
From 1996 to 1997	0.61 ± 0.17	1.29 ± 0.05
From 1997 to 1998	1.71 ± 0.47	0.68 ± 0.02

Table 15
Model selection for variation in availability of graminoid plants in the brood-rearing areas of Banks Island Migratory Bird Sanctuary No. 1 in 1998[a,b]

Model[c]	K	AIC*c*	Δ_i	w_i	r^2
Goose droppings (−)	3	18.4	0	0.99	0.53
Goose droppings (−), Location	6	27.4	9.0	0.01	0.57
No effect (i.e., variation around the grand mean)	2	30.6	12.2	<0.01	n/a
Location	5	37.7	19.3	<0.01	0.12
Goose droppings (−) | Location	10	46.4	27.0	<0.01	0.70

[a] Included in the table are number of model parameters (K), values of Akaike's information criterion adjusted for small sample size (AIC*c*), difference between each model and the best model (Δ_i), model weight (w_i), and model fit (r^2).
[b] Dry masses of both graminoid plants and goose droppings were square root-transformed, as this provided the best linear approximation.
[c] Effects of continuous model variables are indicated in parentheses.

Figure 14
Relationship between goose use and availability of graminoid plants at lake margins in Banks Island Migratory Bird Sanctuary No. 1 in July 1998. Dry masses of both graminoid plants and goose droppings were square root-transformed, as this provided the best linear approximation. Availability of graminoid plants ranged from 0.6 to 94.5 g/m^2.



5. Discussion

5.1 Nesting ecology

5.1.1 Number of nesting geese

We estimated that 264 000–452 000 Lesser Snow Geese nested at Egg River in 1995–1998 and that the nesting population has grown by 4.2% per year since 1953. The number of nesting geese varied considerably among years, however, and was lower in years when nesting was delayed by late snowmelt. A reduction in number of nesting geese in years with late snowmelt was similar to that recorded at Wrangel Island, Russia, where spring chronology was important in affecting the number of geese nesting in each year (Bousfield and Syroechkovskiy 1985). Further, we saw large numbers of nonbreeding geese in the brood-rearing areas in years with late snowmelt, suggesting that timing of snowmelt had a greater effect on the proportion of geese attempting to breed at Egg River each year than it had on the number of geese arriving at Banks Island (for similar observations, see Propp et al. 1984 and Bousfield and Syroechkovskiy 1985). Spring chronology may be especially unpredictable at Egg River, as weather conditions at Banks Island can be very different from those on the mainland before geese cross the Amundsen Gulf (Samelius, pers. obs.). Geese nesting at Egg River may therefore have to wait for snow to melt more frequently or for longer periods than do Lesser Snow Geese nesting at other colonies.

Large annual variation in the number of nesting geese at Egg River differs from limited annual variation in the number of nesting geese as revealed from surveys performed every 5–10 years (see Kerbes et al. 1999 and references therein). Annual variation in number of nesting geese results in variation in recruitment and may also reduce population growth if nesting is delayed in consecutive years, as occurred on Wrangel Island, Russia, where the population of Lesser Snow Geese declined from 150 000 to 56 000 between 1970 and 1975 (Bousfield and Syroechkovskiy 1985; Kerbes et al. 1999). Annual variation in the size of the nesting population should thus be considered when making management recommendations for Lesser Snow Geese nesting on Banks Island.

5.1.2 *Clutch size and drop-eggs*

Clutch size at Egg River was negatively related to timing of snowmelt, which was similar to that recorded at other Lesser Snow Goose colonies where spring chronology is the main factor affecting clutch formation (Mowbray et al. 2000). Late snowmelt may cause female geese to use considerable energy reserves while waiting for snow to melt, which, in turn, results in reduced energy reserves allocated to clutch formation (Ryder 1970; Ankney and MacInnes 1978; Davies and Cooke 1983). Further, delayed nesting is often associated with increased nest parasitism (Bousfield and Syroechkovskiy 1985), which suggests that the negative effect of late snowmelt on clutch formation at Egg River may have been greater than what we detected. In fact, increased rate of egg dropping in late years may function as nest parasitism, as female geese often roll eggs into nests when eggs are located nearby (Mowbray et al. 2000). Thus, the relationship between spring chronology and clutch formation at Egg River was partly unclear, and further research is required to better understand how spring chronology affects clutch formation in this population of geese.

Clutch size at Egg River in 1995–1998 was comparable to that recorded at Egg River in 1955 (McEwen 1958), which suggests that there have been no density-dependent effects on clutch formation, despite an almost 10-fold increase in the number of nesting geese. An apparent lack of density-dependent effects on clutch formation at Egg River differs from that recorded at La Pérouse Bay, Manitoba, where clutch size decreased by 0.72 eggs as the population increased from 3000 to 8000 nesting pairs (Cooch et al. 1989). The apparent lack of density-dependent effects on clutch formation at Egg River suggests that the population was still below levels where density-dependent effects operate or that food availability during spring migration increased during this period (see Cooch et al. 1989). We stress, however, that there may have been other density-dependent effects operating at Egg River that we were unable to detect because of a lack of historical data.

Clutch size at Egg River during this study was comparable to that recorded for Lesser Snow Geese at colonies of similar latitudes (Bousfield and Syroechkovskiy 1985; Alisauskas, unpubl. data), whereas it was smaller than that recorded at La Pérouse Bay, Manitoba, located about 2000 km southeast of Banks Island (Cooke et al. 1995). Latitudinal variation in clutch size may reflect differences in costs of migration or variation in amount of body reserves allocated for successful nest attention during incubation (see Thompson and Raveling 1987). Lesser Snow Geese in northern colonies may, for example, expend more body reserves during migration or allocate less body reserves into clutch formation than geese at southern colonies.

5.1.3 *Nesting success*

Nesting success at Egg River was closely related to timing of snowmelt, which was similar to the pattern of nesting performance by Lesser Snow Geese at other colonies being closely linked to spring chronology (Davies and Cooke 1983; Bousfield and Syroechkovskiy 1985; Alisauskas 2002). Late snowmelt may cause geese to use considerable body reserves while waiting for snow to melt, which, in turn, may result in geese entering incubation in poor condition, with greater risk of abandoning nests (Ankney and MacInnes 1978; Raveling 1979). That depletion of body reserves (followed by increased incubation recess and abandonment) may have caused considerable nesting failure at Egg River was suggested by the high rate of nesting failure in late incubation in years with late snowmelt (see Harvey 1971; Ankney and MacInnes 1978; Raveling 1979). Nest depredation, in contrast, would likely have caused a decreasing rate of nesting failure, as geese generally defend their nests more vigorously as the nesting season progresses (Sjöberg 1994). Similarly, Samelius and Alisauskas (2000) found that fox predation caused a relatively small proportion of nesting failure at Egg River in late years and suggested that factors other than fox predation had more impact on nesting performance in late years. We therefore suggest that timing of snowmelt and, in turn, nutritional dynamics were key factors affecting nesting success at Egg River during this study.

Incubation success at Egg River was comparable to that recorded at other large Lesser Snow Goose colonies (Bousfield and Syroechkovskiy 1985; Alisauskas, unpubl. data), whereas it was generally higher than that recorded at small Lesser Snow Goose colonies, where predation can cause almost complete nesting failure in some years (Bousfield and Syroechkovskiy 1985; Cooke et al. 1995; Armstrong 1998). Predation pressure is generally reduced as colony size increases because of predator swamping, where predators become limited by factors other than food (Wittenberger and Hunt 1985; Raveling 1989). Thus, it is possible that the main factor affecting nesting success by Lesser Snow Geese switches from predation to spring chronology as the nesting population increases.

Nesting failure was highest during egg laying in all years, which may have been related to high nest depredation during this period, when geese are less attentive to nests (as suggested by Klett and Johnson 1982). Absence from nests results in increased risk of nest depredation, where geese that are less attentive to nests lose more eggs to predators than attentive geese (Samelius and Alisauskas 2001; Bêty et al. 2002). Poor nesting survival during egg laying may also have resulted from abandonment by geese in poor condition, which can be prevalent in years with delayed nesting (Ankney and MacInnes 1978; Raveling 1979). Further, flooding of nests also caused reduced nest survival during egg laying in years with late snowmelt (flooding caused 2–13% nesting failure in late years).

5.1.4 *Causes of nesting failure*

Abandonment and nest depredation are generally difficult to separate, because it is often unknown if missing eggs were depredated or scavenged after nests were abandoned (see Larivière 1999). However, even though we could not separate abandonment from nest depredation for most nests, we found that these two parameters caused the majority of nesting failure (87–100%), whereas flooding of nests and mortality of incubating females caused only limited nesting failure (0–13%). Patterns of nesting failure suggested that nesting recess (i.e., "indirect" nest depredation of unattended nests) and abandonment caused the majority

of nesting failure (see section 5.1.3 above), but the influence of different factors affecting nesting performance (e.g., gull versus fox predation) and how these vary among years are poorly understood. Further research is therefore needed to better understand causes of nesting failure for Arctic-nesting geese. Studies that span more years than this study may be especially informative, as nesting failure is a complex process affected by numerous factors.

5.1.5 Adult nesting mortality

We estimated that about 1–4% of the nesting population died at Egg River in 1996–1998 (goose mortality was not monitored accurately in 1995). Avian cholera was confirmed in about half of the dead geese examined for cholera in each year. However, the proportion of geese that died from avian cholera was likely considerably higher, as the analyses were done about 1–2 months after the death of the birds (Samuel et al. 1999). Our estimates of nesting mortality were considerably lower than those reported by Samuel et al. (1999). Differences between estimates may have resulted from differences in methodologies (e.g., our sampling design may not have sampled the clumped outbreak of avian cholera accurately, or goose carcasses from previous years may have been included by Samuel et al. 1999). However, despite differences between studies, they show that several thousand geese died at Egg River each year and that avian cholera caused substantial mortality in this population of birds.

Nesting mortality appeared to be greater in years with late snowmelt, which was also suggested by Samuel et al. (1999), who found that more geese died at Egg River in the late year of 1995 than in the early year of 1996. An apparent link between nesting mortality and spring chronology suggests that deaths may, in part, have been related to depletion of body reserves and nutritional status of geese. Similarly, the chronology of nesting mortality also appeared to be related to timing of snowmelt, with most nesting mortality occurring during late nesting in the early years of 1996 and 1998 compared with early nesting in the late year of 1997. However, the chronology of nesting mortality may, alternatively, have been related to the magnitude of nesting mortality, with most mortality occurring during early nesting in years with greater mortality (i.e., 1997) compared with late nesting in years with less mortality (i.e., 1996 and 1998). Further, geese may also have died both before and after nesting, which, in turn, would have affected both chronology and magnitude of overall mortality (for similar discussion, see Samuel et al. 1999).

5.1.6 Predator abundance and implications

The number of arctic foxes frequenting the colony appeared to be closely linked to lemming abundance, with peak fox abundance following 1 year after peak lemming abundance. Annual variation in goose numbers, in contrast, did not appear to influence fox abundance. A close link between arctic fox dynamics and lemming abundance is similar to that noted in other areas where lemmings, voles, and arctic foxes co-exist (Garrott and Eberhardt 1987; Angerbjörn et al. 1999). Large goose colonies may, however, affect arctic fox dynamics by functioning as sources of fox production, where a superabundance of foods during the nesting season may increase the density or reproductive output of arctic foxes, as suggested by Bantle and Alisauskas (1998). Further research on arctic fox dynamics in relation to large concentrations of birds is needed to better understand how temporarily abundant foods may affect arctic fox dynamics. This may be especially important, as the consequences of the large increase in Lesser Snow Goose numbers in North America are poorly understood (Ankney 1996; Abraham and Jefferies 1997).

Samelius and Alisauskas (2000) estimated that arctic foxes took about 5–10% of the eggs available at Egg River during incubation each year. This rate of fox predation was considerably lower than the rate of predation on Lesser Snow Goose nests by arctic foxes in some years at Wrangel Island, Russia, where almost 100% destruction was observed (Syroechkovskiy and Krechmar 1981 *in* Syroechkovskiy et al. 1991; Bousfield and Syroechkovskiy 1985). Such extreme predation pressure was unusual, however, and occurred only in years with low numbers (<15 000) of nesting geese (Bousfield and Syroechkovskiy 1985). Predation pressure at large goose colonies, such as Egg River, is generally lower than that at small colonies because of predator swamping (Wittenberger and Hunt 1985; Raveling 1989).

The proportion of eggs lost to fox predation during incubation at Egg River was considerably lower than nesting failure in late years (Samelius and Alisauskas 2000), which suggests that spring chronology and depletion of body reserves had greater impact on nesting performance than had fox predation in late years. Further, the majority of eggs lost to foxes were lost when geese were absent from nests or when the male was away feeding (Samelius and Alisauskas 2001), which further illustrates the importance of being in good nutritional condition to successfully complete incubation (see Aldrich and Raveling 1983). Additionally, nesting failure was considerably higher than fox predation in late years, suggesting that there was a large number of eggs left at the colony after hatch upon which foxes and avian predators could scavenge (see Samelius and Alisauskas 1999, 2000).

Samelius and Alisauskas (2000) found that the foraging efficiency of arctic foxes at Egg River was similar among years and suggested that variation in the impact of arctic fox predation reflected changes in the number of foxes frequenting the colony rather than variation in the foraging efficiency of individual foxes. Our observations of a close link between fox numbers and lemming abundance, in turn, suggest that variation in the impact of arctic fox predation at large goose colonies is mediated by variation in lemming abundance and that fox predation is greatest 1 year after peak abundance in lemming numbers (see Bêty et al. 2002 for discussion of the impact of fox predation at a small goose colony).

The number of Glaucous Gulls breeding at Egg River (as indicated by the number of gull nests) was similar among years or perhaps slightly increasing through the study. Further, gull numbers did not follow the large between-year variation in number of nesting geese, despite Glaucous Gulls at large goose colonies feeding almost exclusively on geese and their eggs (Samelius and Alisauskas 1999).

Gull numbers may, instead, have been limited by other factors, such as food availability after goose exodus, winter mortality, or spacing behaviour (see Stempniewics 1995; Samelius and Alisauskas 1999). Avian predators generally do not force geese away from nests (Samelius and Alisauskas 1999; Bêty et al. 2002), which suggests that gull predation of eggs, similar to fox predation, was closely linked to nest attendance and nutritional status of geese (see Ankney 1977; Aldrich and Raveling 1983).

5.2 Brood-rearing ecology

5.2.1 Goose distribution during brood rearing

We estimated that 441 000–644 000 adult Lesser Snow Geese were dispersed throughout Banks Island Migratory Bird Sanctuary No. 1 during the brood-rearing season in 1996–1998. This was 380 000 more geese than we estimated to have nested at Egg River in 1997, which, in turn, suggests that nonbreeding geese and possibly moult-migrants (as suggested by T.W. Barry *in* Kerbes 1986) constitute an important proportion of Lesser Snow Geese using the brood-rearing areas on Banks Island in some years. The presence of large numbers of moult-migrants seems unlikely, as the low proportion of blue geese encountered during the aerial survey is unique to the western Arctic (Mowbray et al. 2000), and moult-migrants from the only other large colony in the western Arctic (i.e., Wrangel Island) moult on Wrangel Island or on the Russian mainland (Syroechkovskiy and Litvin 1986 *in* Ely et al. 1993). Most birds in the brood-rearing areas of Banks Island were, thus, likely from Banks Island.

Years with late snowmelt appeared to be characterized by large numbers of nonbreeding geese (e.g., the number of adult geese in the brood-rearing areas was considerably higher than the nesting population at Egg River in the late year of 1997). There may also have been nonbreeding geese outside of our study area during the aerial survey (e.g., Barry [1960] found failed and nonbreeding geese at the Thomsen River at the northern end of the island), suggesting that a substantial portion of the adult population on Banks Island was composed of nonbreeding birds (i.e., subadult geese and adult geese in poor condition) in some years. Further, Lesser Snow Geese appear to start breeding at an older age at northern latitudes (Ganter et al., 2005), so spring chronology and delayed nesting may act in concert to influence the proportion of nonbreeding geese on Banks Island. The adult population of Lesser Snow Geese on Banks Island was thus considerably larger than the population that nested at Egg River in some years, which, in turn, will have implications for recommendations on harvest rates and overall population dynamics. We recommend a complete survey of the island to evaluate the total number of Lesser Snow Geese on Banks Island and to better understand the distribution of geese on the island. A complete survey of the island may be linked to muskox surveys (e.g., Larter and Nagy 2001) for cost-efficiency.

Breeding geese remained closer to Egg River during the brood-rearing period than failed and nonbreeding geese; the highest densities of breeding geese were found in the river valleys from Lennie River up to Storkerson River, whereas failed and nonbreeding geese were found in the highest density in the delta of Bernard River, about 125 km north of Egg River. Even though densities generally were lower on the uplands, its vast area (80% of the study area) resulted in most geese being associated with ponds, lakes, creeks, and small rivers on the uplands. Dispersal of breeding birds farther from the colony in 1996 and 1998 may have been related to differences in the numbers of nesting geese and proportions of young hatched.

5.2.2 Index of gosling survival

We estimated that 27–44% of the goslings that left Egg River survived the first 2–3 weeks after hatch in 1996–1998. We suggest that weather as well as predation were important factors affecting gosling survival on Banks Island. Cold, wet weather from the Beaufort Sea may reduce gosling survival on Banks Island. We observed a few instances of arctic foxes and snowy owls attacking goose broods during our aerial surveys. Two of these attacks were successful; a snowy owl took one gosling in 1996, and a fox took one gosling in 1998. In 1998, we observed a fox following a flock of breeding geese about 5 m into a pond before returning to shore without capturing any geese. Heavy grazing by geese (see section 5.4.2 below) and, thus, food shortage did not appear to affect gosling survival, because goslings seemed healthy and in good condition at about 3–4 weeks of age (Hines, pers. obs.). Female Lesser Snow Geese from Banks Island were, however, smaller than those from Karrak Lake, Nunavut, which may have reflected variation in food availability between these locations during the time of gosling growth (see Cooch et al. 1991; Francis et al. 1992).

Our estimate of gosling survival at the age of 2–3 weeks was similar to that recorded for Lesser Snow Goose goslings at 4–5 weeks of age at other colonies (Williams et al. 1993; Slattery 1994). However, most gosling mortality generally occurs within the first few weeks after hatch (Williams et al. 1993), which, despite differences in the age of goslings between our and other studies, suggests that gosling survival at Banks Island was similar to or perhaps somewhat lower than that at other Lesser Snow Goose colonies.

5.3 Population growth rate

The number of Lesser Snow Geese nesting on Banks Island has grown by 4.2% per year since 1953; however, the annual growth rate at Banks Island was lower than that of Lesser Snow Geese breeding in the central and eastern Canadian Arctic (see Abraham and Jefferies 1997; Alisauskas 2001). The lower growth rate of the Banks Island population may, in part, be related to large annual variation in the number of geese nesting at Egg River and reduced recruitment following years with delayed snowmelt (see Bousfield and Syroechkovskiy 1985). Further, Lesser Snow Geese appear to start breeding at an older age at northern latitudes (Ganter et al. 2005), so delayed breeding may further impinge upon the growth rate of the Banks Island population. Annual rate of change in the nesting population and the adult population in the brood-rearing areas showed opposite trends, and the magnitude of change

in one parameter appeared to be unrelated to the magnitude of change in the other. This illustrates that between-year estimates of population change for one section of the population cannot be used to estimate between-year variation in another section of the population (e.g., surveys of the nesting population will not provide an estimate of the overall population, and vice versa).

5.4 Impact of grazing

5.4.1 Plant cover at Egg River

Plant cover at Egg River was negatively correlated with nesting density, whereas cover by marsh ragwort (an indicator of overgrazing; Jefferies and Abraham 1994) was positively correlated with nesting density. These patterns of plant cover suggest that geese influence the plant community at Egg River. Negative effects on plant cover may be a correlate of nesting habitats by geese (i.e., preferred nest sites or sites where snowmelt is early may have different plant cover than less preferred habitats or habitats where snowmelt is late), whereas a positive correlation between nesting density and cover by marsh ragwort suggests that grazing by geese affected the plant community at the Egg River colony.

5.4.2 Goose use and availability of graminoid plants in the brood-rearing areas

There was a strong negative correlation between goose use and availability of graminoid plants in the brood-rearing areas on Banks Island, where areas with high use were heavily grazed. Heavy grazing by geese was further suggested by areas with high goose use having well below 25 g of aboveground biomass per square metre, which may indicate overgrazing or that habitats have been partially destroyed by grubbing (Jefferies and Abraham 1994). However, we saw no evidence of permanent destruction of habitats, so the influence of grazing and how plant communities respond may thus vary between geographic regions and between habitats such as salt marshes along Hudson Bay (e.g., Jefferies and Abraham 1994) and lake margins at Banks Island. Heavy use of lake margins on Banks Island may, however, have reflected the smaller size of female Lesser Snow Geese on Banks Island compared with that recorded at Karrak Lake, Nunavut (see Cooch et al. 1991; Francis et al. 1992).

Geese used lake margins and snowpatch fens with similar intensity, even though there was a trend for geese to use lake margins more frequently than snowpatch fens. Similar use of habitats may have been a consequence of small sample size (n = 5 matched samples) or a switch to use habitats farther from lakes as goslings grew older (see Hughes et al. 1994; Jefferies and Abraham 1994). Ponds and lakes often function as predator refuges in brood-rearing areas (Giroux et al. 1984; Hughes et al. 1994), and we observed geese moving onto water when approached by arctic foxes during aerial surveys. Pond and lake margins also provide an important source of high-quality foods for growing goslings (Jefferies and Abraham 1994).

5.5 Management implications

The Lesser Snow Goose population on Banks Island has grown considerably since the 1980s and is currently about twice as large as it was two decades ago (see Kerbes et al. 1999); we therefore recommend continued monitoring of this population to examine for potential density-dependent effects on productivity, such as that recorded on clutch formation at La Pérouse Bay, Manitoba (Cooch et al. 1989). Further, the growth rate of the Lesser Snow Goose population on Banks Island was lower than that of Lesser Snow Geese breeding in the central and eastern Canadian Arctic (e.g., Abraham and Jefferies 1997; Alisauskas 2001), which also illustrates the need to continue monitoring the Banks Island population to gather accurate information with which to manage this population (see Kerbes et al. 1999 for a similar recommendation). Abundance of geese can be monitored by aerial surveys, following Kerbes et al. (1999), whereas monitoring of both abundance and productivity requires groundwork similar to that of this study. Further, aerial surveys combined with groundwork will help to develop correction factors such as detection probability for aerial photographs.

Productivity of Lesser Snow Geese from Banks Island varied considerably among years, with more goslings produced in years with early snowmelt than in years with late snowmelt. We suggest that the negative effect of late snowmelt on the productivity of young was related to the use of body reserves while waiting for the snow to melt (Ankney and MacInnes 1978; Raveling 1979) and that spring chronology and, in turn, body condition and nutrient dynamics were key factors affecting productivity of goslings on Banks Island (see Davies and Cooke 1983; Alisauskas 2002). We therefore recommend that spring chronology, nutrient dynamics, and annual variation in productivity of young should be considered when making management recommendations for Lesser Snow Geese nesting on Banks Island.

Areas with high goose use were heavily grazed, and we recommend further studies on habitat use and impact of goose grazing to better understand how goose grazing influences productivity of geese on Banks Island. This may be especially important, as the Lesser Snow Goose population on Banks Island has grown considerably during the last three decades, and there are alarming reports of population growth and overgrazing by geese in the eastern Canadian Arctic (Kerbes et al. 1990; Ankney 1996; Abraham and Jefferies 1997).

6. Conclusion

This study showed that timing of snowmelt appeared to be the main factor affecting nesting performance (e.g., number of nesting geese and nesting success) and productivity of Lesser Snow Geese at Egg River. Spring chronology is important in affecting nesting performance of Lesser Snow Geese at other colonies (Davies and Cooke 1983; Bousfield and Syroechkovskiy 1985; Alisauskas 2002), which, in turn, appears to be related to depletion of body reserves while waiting for snow to melt (Ankney and MacInnes 1978; Raveling 1979). We suggest that spring chronology may be especially unpredictable at Egg River, as weather conditions at Banks Island can be very different from those on the mainland before crossing the Amundsen Gulf (Samelius, pers. obs.). Nest depredation by arctic foxes was considerably lower than nesting failure in late years (Samelius and Alisauskas 2000), which suggests that depletion of body reserves and abandonment had a greater impact on nesting performance than had fox predation in late years. Further, depletion of body reserves affects nesting performance indirectly by geese taking more incubation breaks, which, in turn, results in greater risk of egg loss to arctic foxes and avian predators (see Samelius and Alisauskas 1999, 2001; Bêty et al. 2002).

This study showed that the highest densities of Lesser Snow Geese in the brood-rearing areas of Banks Island Migratory Bird Sanctuary No. 1 were concentrated in the major river valleys from Kellett River to Bernard River. However, the vast area of the uplands between these large river valleys resulted in most geese being associated with small bodies of water (e.g., creeks, small rivers, ponds, and lakes) on these uplands. Further, failed and nonbreeding geese dispersed farther than brood-rearing geese. Brood-rearing areas with high densities of geese were heavily grazed, even though we did not observe any evidence of permanent destruction of habitats. Gosling survival averaged 38% during the first 2–3 weeks after hatch and appeared to be similar to or somewhat lower than that recorded at other Lesser Snow Goose colonies (Williams et al. 1993; Slattery 1994). We were unable to address factors affecting gosling survival, and we suggest that this is currently the main information gap relating to factors affecting productivity of Lesser Snow Geese on Banks Island.

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Appendices

Appendix 1
Surface area for strata of the aerial surveys of Banks Island Migratory Bird Sanctuary No. 1 in 1995–1998[a]

Location	Area (km²)
Kellett River	89
Lennie River	58
Big River and Sea Otter River	926
Storkerson River	547
Satchik River	84
Bernard River, delta	283
Bernard River, rest	1 633
Uplands	14 435

[a] Uplands were not sampled in 1995.

Appendix 2
Plant cover at the Egg River colony on 29 June to 1 July 1998[a]

Plant or other material	Cover ± 95% CI (%)
Mountain avens (*Dryas* spp.)	21.5 ± 1.8
Mosses (phylum Bryophyta)	21.2 ± 1.8
Willows (*Salix* spp.)	15.2 ± 1.6
Graminoid plants (families Gramineae and Cyperaceae)	3.8 ± 0.8
Lichens[b]	2.1 ± 0.6
Marsh ragwort (*Senecio congestus*)	0.9 ± 0.4
Arctic heather (*Cassiope tetragona*)	0.3 ± 0.2
Unidentified plants	1.8 ± 0.5
Sand and clay	26.9 ± 1.9
Gravel	4.3 ± 0.8
Peat	1.6 ± 0.5
Rock	0.2 ± 0.2
Water (<10-m-wide ponds)	0.2 ± 0.2

[a] Plant cover was sampled 7–9 days after peak hatch and 30–32 days after the first flowering of purple saxifrage, which was used as an indicator of spring phenology. Plant cover was 66.8% (± 2.0%), whereas other material covered 33.2% (± 2.0%) of the colony.
[b] Lichens reported here were fruticose and foliose lichens (i.e., lichens with upright growth) growing on sand and clay; crustose and squamulose lichens (i.e., crust-like lichens) were common on gravel, but not reported here.

Appendix 3
Body measurements of Lesser Snow Geese collected at the spring hunt in Sachs Harbour in 1997 and 1998[a]

	Adult plumage						Juvenile plumage					
	Females			Males			Females			Males		
Measurement	Mean	95% CI	*n*	Mean	95% CI	*n*	Mean	95% CI	*n*	Mean	95% CI	*n*
Mass (kg)	2.58	± 0.09	18	2.52	± 0.10	23	1.88	± 0.60	3	2.23	± 0.19	4
Abdominal fat (g)	106	± 8.5	18	80.4	± 13.7	23	48	± 41	3	84	± 98	3
Protein index (g)[b]	699	± 37	18	716	± 28	23	543	± 171	3	651	± 85	4
Breast weight (g)[b]	210	± 12	18	209	± 12	23	158	± 42	3	193	± 23	4
Leg weight (g)[b]	74.3	± 5.3	18	90.1	± 5.3	23	60.7	± 27.5	3	77.0	± 17.5	4
Liver weight (g)	41.1	± 3.3	18	29.3	± 2.9	23	21.7	± 13.7	3	26.2	± 9.8	4
Heart weight (g)	25.4	± 2.2	17	26.1	± 1.9	22	18.3	± 1.4	3	22.0	± 3.2	4
Gizzard weight (g)[b]	130	± 8	18	117	± 7	23	106.3	± 37.3	3	112	± 28	4
Ovary weight (g)	31	± 11	18	n/a	n/a	n/a	[c]	[c]	[c]	n/a	n/a	n/a
Tarsus length (mm)	78.2	± 1.4	18	81.6	± 1.2	21	79.6	± 9.0	3	83.6	± 7.2	4
Skull length (mm)	112	± 2	18	116	± 1	22	108	± 6	3	115	± 4	4
Skull width (mm)	37.3	± 0.8	18	38.4	± 0.8	21	34.1	± 2.7	3	37.1	± 1.8	4
Cranial height (mm)	47.3	± 1.0	18	49.5	± 0.8	22	44.9	± 8.0	3	48.8	± 3.2	4
Culmen (mm)	50.8	± 1.2	18	52.2	± 1.2	22	48.0	± 2.8	3	53.3	± 2.2	4
Culmen 2 (mm)	63.3	± 1.5	18	66.0	± 1.1	22	60.2	± 5.6	3	66.2	± 4.0	4
Wing span (m)	1.36	± 0.04	6	1.40	± 0.04	12	1.30	± 0.18	3	1.40	± 0.05	4
Wing chord (mm)	415	± 5	18	427	± 5	21	384	± 203	2	410	no data	1

[a] Geese were collected on 20–22 May in 1997 and on 17–21 May in 1998. Body measurements followed Dzubin and Cooch (1992).
[b] Protein index is the sum of the mass of breast muscles, leg muscles, and the gizzard. Discrepancies between protein index and the sum of [(breast and leg muscle times two) plus gizzard] are due to rounding of numbers.
[c] Ovary weight of juvenile females was not recorded.

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